VOL. 19, No. 3 MARCH 11, 1940

MEMOIRS OF THE TORREY BOTANICAL CLUB

Editor

R. P. Wodehouse

Associate Editors

A. F. Blakeslee, Ph.D. R. A. Harper, Ph.D.
F. E. Denny, Ph.D. J. S. Karling, Ph.D.
H. A. Gleason, Ph.D. E. W. Sinnott, Ph.D.

Studies in the Cichorieae

Dubyaea and Soroseris, Endemics of the Sino-Himalayan Region

By

G. LEDYARD STEBBINS, JR.

Division of Genetics
University of California
Berkeley, California

Published for the Club by
George Banta Publishing Company
Menasha, Wisconsin

Botany
Direct
4-30-40

Table of Contents

I. Introduction 5

II. Key to the Sino-Himalayan genera of Cichorieae 6

III. The Genus Dubyaea 8
- History of the Genus
- Revised Generic Description
- Relationships of Dubyaea
- Diagnosis of Sections
- Artificial Key
- Sec. 1 Eudubyaea
- Sec. 2 Ixeridopsis
- Sec. 3 Amoenae

IV. The Genus Soroseris 27
- Generic Description
- Diagnosis of Sections
- Artificial Key

V. Lactuca, Sec. Aggregatae 47

VI. Distribution 50
- A. Dubyaea
- B. Soroseris

VII. Floral Anatomy 55
- Dubyaea and Soroseris

VIII. Some Histological Characteristics of Dubyaea and Soroseris 64

IX. Cytology of the Species 68

X. Phylogenetic Relationships of the Genera 71

Literature cited 75

Studies in the Cichorieae: Dubyaea and Soroseris, Endemics of the Sino-Himalayan Region

G. Ledyard Stebbins, Jr.

I. INTRODUCTION

The fruitful results of the combined cytogenetic and systematic studies which Professor E. B. Babcock has conducted for the last twenty years on the genus *Crepis* have amply demonstrated the excellence of this material for this work. In order to provide a background for these studies, and to understand what relation the evolutionary processes in *Crepis* bear to the broader problems of the evolution of the larger plant groups, an examination is necessary of the relatives of this genus, particularly those which might represent or be related to its actual ancestors. A preliminary effort in this direction was made by Babcock (1936) in connection with a survey of phylogenetic trends in *Crepis* itself. He suggested that the most probable center of origin for the genus was south central Asia, and cited as the nearest living relative of its ancestors a species of the northwestern Himalaya, which was then known as *Paleya oligocephala*. He also pointed out the significance of the occurrence in this region of a small group of species, usually treated as the Section Glomeratae of *Crepis*, which appeared to show affinities to both *Crepis* and *Prenanthes*.

As a continuation of this work, the present author is making a survey of the genera of the Compositae, tribe Cichorieae related to *Crepis*, and has given particular attention to the groups centering about or near the hypothetical center of origin for *Crepis*, Central Asia. Early in the progress of this survey the existence of a genus related to *Crepis* and endemic to the Sino-Himalayan mountain region was postulated (Stebbins 1937). This genus, which is a redefinition of DeCandolle's genus *Dubyaea*, was found to include the two primitive relatives of *Crepis*, *D. hispida* (*Lactuca* or *Crepis Dubyaea*) and *D.* (*Paleya*) *oligocephala*, and in addition four species previously referred to *Lactuca*. Further studies of *Dubyaea* have amply justified its claim to generic rank, and have added three species to the number recognized. In addition the opinion of Babcock (1936), that the anomalous group of the Glomeratae do not belong in *Crepis* has been fully verified, but their retention in *Prenanthes* has proved equally untenable. Instead they constitute a genus by themselves, endemic to the Sino-Himalayan region and Tibet, which is most closely related to *Dubyaea*. The present work is a systematic monograph of these two genera, together with a consideration of their position in the tribe Cichorieae. A third group, consisting of three anomalous species of *Lactuca*, has been confused

by previous botanists with the GLOMERATAE, and is therefore included in the systematic treatment.

This study has brought to light much evidence concerning the origin not only of *Crepis*, but in addition of four or five other genera of the Cichorieae: *Prenanthes*, *Lactuca*, *Youngia*, *Ixeris*, and perhaps *Hieracium*. For this reason, some general discussion of the relationships of these genera has been made. In addition, the distribution of the species of these genera has provided additional evidence on some of the interesting phytogeographic problems connected with this region, a part of which has been aptly termed "one of the botanical treasure houses of the world" (Ward 1935, p. 263). These problems, therefore are given special attention in the section on distribution.

This study was based on the specimens in the Herbarium of the University of California (UC) and in the following herbaria, loaned to the author through the generosity of their curators: Botanical Museum and Gardens, Berlin (B); Forest Research Institute, Dehra Dun, India (DD); Royal Botanic Garden, Edinburgh (E); Gray Herbarium, Harvard University (G); Royal Botanic Gardens, Kew (K); Natural History Museum, Vienna (V); New York Botanical Garden (NY); Smithsonian Institution, Washington (US). The author gratefully acknowledges with many thanks the privilege of borrowing these specimens. He is particularly indebted to Professor E. B. Babcock for his advice and criticism throughout the work. Helpful suggestions have also been received from Dr. H. Handel-Mazzetti. The author, however, assumes full responsibility for both the systematic treatment adopted and the conclusions reached in the general sections. The drawings were prepared by Mrs. Katherine D. Jenkins, except for portions of Figures 2 and 3, which are the work of Miss Anna Hamilton. The author is much indebted for their painstaking care in the work. Grateful acknowledgment is also made for the partial support of this investigation from the following institutions: Rockefeller Foundation; Carnegie Institution of Washington; Board of Research of the University of California; American Philosophical Society.

II. KEY TO THE SINO-HIMALAYAN GENERA OF CICHORIEAE

In order to orient the reader on the interrelationships of the tribe Cichorieae in this region as conceived by the present author, and to provide a ready means of identifying plants as belonging to the groups to be considered, an artificial key to these genera as they occur in the Sino-Himalayan region is presented. It should be noted that the generic characters as used in this key do not necessarily apply to species which are not found in the region under consideration. The genus *Faberia* is not included

in the key since, in the opinion of the author, it is not generically distinct from *Prenanthes*. A discussion of this group will be made in a later publication.

A. Pappus none or rarely uncinate.....*Lapsana*

A. Pappus present, setose.

B. Pappus setae plumose.

C. Plants glabrate or floccose-tomentose; plumes of pappus setae long, interlaced.....*Scorzonera*

C. Plants setose-hispid; plumes of pappus setae not interlaced.....*Picris*

B. Pappus setae not plumose.

D. Achenes tuberculate or muricate on the surface, at least on the upper portion.

E. Plants with well-developed, branched stems.....*Chondrilla*

E. Plants acaulescent, the heads borne on hollow scapes.....*Taraxacum*

D. Achenes smooth, scabrous, spiculate, or rugose.

E. Achenes strongly obcompressed, with 2–4 principal ribs; ovary with 2–4 principal vascular bundles; at least some of the pappus setae only 2- or 4-celled in cross section at the base.

F. Involucres with 80 or more florets; pappus setae of two very dissimilar types, some relatively coarse and straight, others very fine and flexuous, 2–4-celled in cross section, causing the pappus to adhere to clothing, etc.....*Sonchus*

F. Involucres with 3–30 or rarely up to 50 florets; pappus setae relatively uniform, all more or less straight, often brittle.....*Lactuca*

E. Achenes terete or slightly obcompressed, with 5–10 principal ribs; ovary with 5–20 vascular bundles.

G. At least some of the pappus setae only 4-celled in cross section at the base; corollas small and delicate, the tube elongate, distinctly exceeding the ligule; stigmatic branches slender and pale.....*Lactuca* spp.

G. All of the pappus setae more than 4-celled in cross section at the base (except in a few species of *Launaea* and *Crepis*); corolla tube sometimes slightly exceeding, but mostly equalling or shorter than the ligule.

H. Involucral bracts more or less evenly imbricated, the outer passing gradually into the inner.

I. Heads with 8–12 florets; achenes pale buff or somewhat greenish, the principal ribs thick and corky.....*Launaea*

I. Heads with 10 or more, mostly very many florets; achenes yellowish, reddish, or blackish, the ribs relatively slender and closely spaced.

J. Stigmatic branches terete, 0.1–0.14 mm. broad, achenes terete, with 10–15 equal ribs, truncate at the apex..*Hieracium*

J. Stigmatic branches somewhat flattened, 0.16–0.3 mm broad; achenes slightly obcompressed, unequally ribbed, or with 5 widely spaced, slender ribs, more or less attenuate at the apex or with a short, thick beak.....*Dubyaea*

H. Involucral bracts consisting of a distinct inner and outer series.

K. Tufted alpine plants, the heads crowded in a glomerate inflorescence; outer involucral bracts narrowly linear, slightly shorter than to exceeding the inner; inner involucral bracts coalescent at the base; receptacle concave. *Soroseris*

K. Plants of various habit; outer involucral bracts deltoid or lanceolate, mostly $\frac{1}{3}$ to $\frac{1}{2}$ as long as the inner; inner bracts distinct from each other; receptacle flat or convex.

L. Mostly tall or climbing plants of mesophytic situations; flowers purplish, bluish or whitish, never yellow; corolla tube about equalling or somewhat exceeding the ligule; stigmatic branches blackish, somewhat flattened, 0.16–0.26 mm broad; achenes truncate or rarely attenuate at the apex.....*Prenanthes* (incl. *Faberia*)

L. Flowers yellow or whitish (except in some species of *Ixeris*, which have long-beaked achenes); corolla tube distinctly shorter than the ligule; stigmatic branches yellowish, terete, 0.14 mm or less in diameter (blackish and flattened only in *Youngia* sect. *Desiphylum*, a group of dwarf alpines); achenes attenuate at the apex or beaked.

M. Achenes terete, equally ribbed.....*Crepis*

M. Achenes somewhat obcompressed.

N. Achenes unequally ribbed, the ribs obtuse, usually not beaked.....*Youngia*

N. Achenes equally ribbed, the ribs often acute or alate, distinctly beaked.....*Ixeris*

III. THE GENUS DUBYAEA

HISTORY OF THE GENUS

The genus *Dubyaea* was first constituted by De Candolle (Prodr. 7: 247) to include three species; *D. cristulata* of New Holland, *D. hispida* of the Himalaya, and *D. sonchoidea* of Armenia. It was named in honor of J. E. Duby, a contemporary French botanist who prepared the monograph of *Primula* for the Prodromus. I have not seen any specimens of *D. cristulata*, and, so far as I am aware, this species has not been mentioned in any subsequent publications. It is presumably a species of *Sonchus*, and perhaps *S. grandifolius* Hook. f. *D. sonchoidea*, based on *Lasiopus sonchoides* Don, is *Taraxacum montanum* DC. The third species, *D. hispida*, was based on *Hieracium hispidum* Wall. This species was transferred by C. B. Clarke (Comp. Ind. 271) to *Lactuca*, as *L. Dubyaea*. Clarke was apparently influenced by the presence of compressed (or obcompressed) achenes, and the resemblance between the involucres of this species and those of *L. Lessertiana* (Wall.) Clarke. Hooker (Fl. Brit. India 3:409) erected for the species the section DUBYAEA of *Lactuca*. This treatment was followed by all later writers on the Sino-Himalayan flora until recent years, as well as by Hoffmann in "Die Natürlichen Pflanzenfamilien" (vol. 4, pt. 5: 372). Franchet in 1895 (Jour. de Bot. 60: 294) and W. W. Smith in 1920 (Notes Bot. Gard. Edinb. 12: 211) each added a species to this section. In 1916 Hutchinson (Kew Bull. 189) described *Crepis*

bhotanica, the type of which is unquestionably *D. hispida*, while in 1929 Marquand and Shaw (Jour. Linn. Soc. 48: 194) transferred the same species to *Crepis* as *C. Dubyaea*, without comment. Their disposition of the species was generally accepted by later writers. Handel-Mazzetti described in 1924 (Sitzganz. Akad. Wiss. Wien 61: 23) a new section of *Lactuca*, Sect. AMOENAE, which on the basis of its involucral and floral characteristics he placed next to the sect. DUBYAEA, but which differed strikingly from that section in habit and in the shape of the heads. In 1936 (Symb. Sin. 7(4): 1182) he retained this section as well as Franchet's species of the section DUBYAEA, *L. atropurpurea*, in *Lactuca*, but placed *Dubyaea hispida* (*L. Dubyaea*) in *Crepis*. He did not give any reason for segregating the species of the Sect. DUBYAEA, *D. hispida* and *D. atropurpurea*, into two different genera, but suggested an affinity of Sect. AMOENAE to *Lactuca atropurpurea*. In 1937 (Jour. Bot., 75 p. 17) the writer pointed out the difficulty of referring all of these obviously interrelated species either to *Lactuca* or to *Crepis*, and suggested that De Candolle's genus be reconstituted for them.

REVISED GENERIC DESCRIPTION

Dubyaea DC., Prodr. 7: 247, 1838. (Compositae-Cichorieae). Herbaceous perennials with milky juice; leafy stemmed or acaulescent; leaves various in size and shape; inflorescence cymose or racemose, of few heads, or heads solitary; involucres large, broadly or narrowly campanulate, 10–80 flowered; involucral bracts numerous, rather evenly imbricated, not at all thickened at maturity; corollas large, completely glabrous, the tube shorter than the ligule; anthers short-caudate, blackish or yellowish; style with numerous and conspicuous barbs ("collecting hairs") below the branches of the stigma; stigmatic branches linear, flattened, 1–3 mm long, 0.16–0.3 mm broad, covered with barbs on the outer surface, evenly papillate on the inner surface, style and stigmas mostly blackish or greenish on the upper portion; achenes fusiform, in some species short-rostrate, in others nearly truncate at the apex, slightly obcompressed, with 5–10 prominent ribs and usually 1–6 lesser ones; pappus setae coarse, rigid; receptacle plane or somewhat convex, shallowly or deeply pitted, the margins of the pits plane or erose, not ciliate; receptacular paleae absent. Basic chromosome number probably $x=8$.

Nine species, natives of western China and the Himalaya Mountains, mostly in alpine or subalpine situations. Type species *Dubyaea hispida* (Don) DC. (*Hieracium hispidum* Don).

RELATIONSHIPS OF DUBYAEA

The genus *Dubyaea* shows a definite relationship to most of the larger genera of the tribe Cichorieae which have a capillary pappus (subtribe

Crepidinae of Hoffmann, Planzenfamilien 5(4): 366). To *Lactuca*, with which genus *Dubyaea* has been united by most authors, the resemblance is chiefly in habit. *D. atropurpurea* (Franch.) Stebbins is very similar in general appearance to *Lactuca atropurpurea* Franch. (*L. grandiflora* Fr.), as well as to *L. macrantha* Clarke. *Dubyaea* differs from *Lactuca*, however, in having only slightly flattened achenes, which contain five main vascular bundles and a number of lesser ones, and in its much coarser pappus setae, most of which are more than four cells in cross section for practically their entire length, and may therefore be said to lack terminal trichomes (Babcock and Stebbins 1937, p. 7) (cf. Figure 1). *Lactuca atropurpurea* and *L. macrantha*, have strongly flattened achenes with 2–4 main vascular bundles and the relatively weak pappus bristles characteristic of *Lactuca* (Stebbins 1937, pp. 13–14). The bulk of the species of *Lactuca*, furthermore, differ widely from *Dubyaea* in their relatively small and numerous heads, their smaller and more delicate corollas, their slender, terete, and pale stigmatic branches, and their much more strongly flattened achenes.

Between *Crepis* and *Dubyaea* there is an equally close connection. *Dubyaea hispida* (Don) DC. and *D. oligocephala* (Sch. Bip.) Stebbins are similar in habit respectively to *Crepis kashmirica* Babcock and *C. sibirica* L. These species of *Crepis* also have the coarse pappus bristles and the floral anatomy characteristic of *Dubyaea*. They differ, however, in possessing the slender, terete, and yellow stigmatic branches (Figures 7, 8) as well as the terete, evenly ribbed achenes characteristic of *Crepis*. From the bulk of *Crepis* species, *Dubyaea* differs also in its larger heads with more numerous, evenly imbricated involucral bracts, in its larger florets and achenes, and coarser pappus setae.

The connection between *Dubyaea* and *Youngia* has already been pointed out (Babcock and Stebbins 1937, pp. 15–16). *Youngia* differs from *Dubyaea* in its smaller, narrower involucres, of which the bracts are divided into a distinct outer and inner series, the former being much shorter and deltoid. Furthermore all of the sections of *Youngia* except Sect. DESIPHYLUM have, like most *Lactuca* and *Crepis* species, much smaller florets and achenes, and less coarse pappus bristles then *Dubyaea*. The genus *Ixeris*, a close relative of *Youngia*, shows a similar relationship to *Dubyaea*. *D. chimiliensis* (W. W. Smith) Stebbins, in particular, resembles *Ixeris* in its glabrous habit, lanceolate, entire leaves, and in the color and beaked character of its achenes. The species of *Ixeris* most nearly related to *Dubyaea* is *I. alpicola* Nakai of Japan, but there is also a connection between *Dubyaea chimiliensis* and *Ixeris laevigata* (DC.) Stebbins through the anomalous *Youngia silhetensis* (DC.) Babcock and Stebbins. The generic position of the latter species is still in doubt; morphologically it stands midway be-

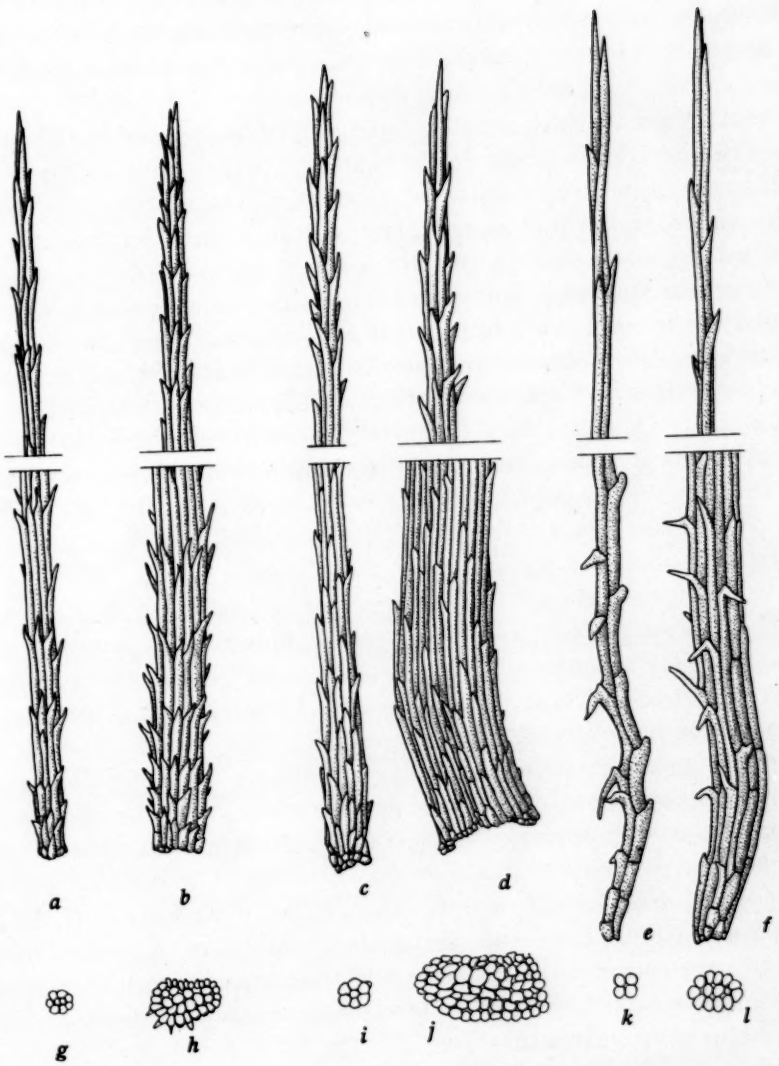

Fig. 1. *a–f*. Side views of the basal and apical portions of the weakest and strongest pappus setae of: *a*, *b*, *Dubyaea chimiliensis; c*, *d*, *Soroseris rosularis; e*, *f*, *Lactuca disciformis*. *g–l*, cross sections at the base of the weakest and strongest pappus setae of: *g*, *h*, *Dubyaea atropurpurea; i*, *j*, *Soroseris Deasyi; k*, *l*, *Lactuca disciformis*. All ×100.

tween *Dubyaea chimiliensis* and *Ixeris laevigata*. It resembles the former in its coarse pappus setae and unequally ribbed achenes, and the latter in habit, as well as its small, narrow involucres whose bracts are in two series. Its diagnostic characters place it in *Youngia*, and emphasize further the close connection between *Youngia* and *Ixeris*.

Another genus which shows a close affinity to *Dubyaea* is *Prenanthes*. These two genera are similar in the character of their corollas, styles, and stigmas, in their slightly flattened achenes, in the vascular anatomy of their ovaries, and in their coarse pappus setae. *Prenanthes*, however, has more numerous, smaller and mostly fewer flowered involucres, of which the bracts are sharply differentiated into two series, while its achenes are in most species cylindric and truncate at the apex, rather than fusiform. The species of *Prenanthes* nearest to *Dubyaea* both in habit and in the size of the involucres is *P. crepidinea* Michx. of the eastern United States, but *P. ochroleuca* (Maxim.) Hemsl. and *P. acerifolia* (Maxim.) Matsumura, both of Japan, also show some resemblances to *Dubyaea*. It is an interesting fact that *Prenanthes*, which is closer to *Dubyaea* in floral characteristics than is any other genus, nevertheless deviates more from it in habit than do certain species of *Lactuca*, *Crepis*, and *Youngia*.

Dubyaea also shows a definite relationship to *Hieracium*. *D. glaucescens* Stebbins resembles *Hieracium* in its yellow, uniseriate pappus and more or less truncate achenes, while the deltoid, evenly imbricated involucral bracts are not unlike those of some species of *Hieracium* sub. *Archieracium*. *D. glaucescens* however, has purple flowers, which are not known in *Hieracium;* its stigmas are broader, and its achenes are typical of *Dubyaea* in being unequally ribbed, while those of *Hieracium* are terete and equally ribbed. *Dubyaea tsarongensis* (W. W. Smith) Stebbins, furthermore, shows a resemblance both in habit and in the character of its corollas, achenes and pappus to *Hieracium Krameri* Franch. & Sav. of Japan, and *H. Nakaii* Kitagawa of Korea. These two species are somewhat anomalous in *Hieracium*, but are connected with the rest of the genus through *H. hololeion* Maxim. *Hieracium*, however, is definitely more remote from *Dubyaea* than are the other genera mentioned.

Dubyaea somewhat resembles *Sonchus* in habit, and in the size and character of its involucres, but in other characteristics the two genera are rather remote from each other. There is also a habital resemblance between *Dubyaea* and certain species of *Hypochaeris*, such as *H. grandiflora* Ledeb., which has in addition achenes similar in shape and ribbing to those of *Dubyaea*. This may signify a real relationship, although the paleae on the receptacle and the character of the pappus, as well as the slender, yellow stigmatic branches contrast sharply with the characteristics of

Dubyaea. The close connection between *Dubyaea* and another Cichoriaceous genus endemic to the Sino-Himalayan region will be discussed below.

Dubyaea, therefore, shows affinities to a number of the well known, widespread genera of the Cichorieae. The phylogenetic significance of these relationships will be discussed in a later section of this paper.

DIAGNOSIS OF SECTIONS

SECTION 1. **Eudubyaea,** sec. nov.—Stout, leafy stemmed perennials, hirsute or glabrous; leaves mostly lyrate, runcinate, or sinuate pinnatifid, or at least strongly dentate; involucres large, broadly campanulate, with 40–80 florets; involucral bracts numerous, deltoid or lanceolate; flower color various; pappus setae yellowish, cream color, or white. Type species, *D. hispida* (Don) DC.

SECTION 2. **Ixeridopsis,** sect. nov.—Slender perennials, leafy-stemmed or scapose, glabrous; leaves lanceolate or oblanceolate, the margins entire; involucres broadly campanulate, with 20–35 florets; involucral bracts loosely imbricated, broadly oblanceolate or narrowly elliptic; flowers bright yellow; pappus yellowish. Type species, *D. tsarongensis* (W. W. Smith) Stebbins.

SECTION 3. **Amoenae** (Hand.-Mazz.) comb. nov.—Acaulescent perennials, hirsute or glabrous, the leaves all basal, pinnatifid or entire; scapes naked or bracteate; involucres narrowly cylindric-campanulate, with 10–17 florets; involucral bracts deltoid or lanceolate; flowers blue or bluish purple; pappus setae rufous. (*Lactuca* Sect. AMOENAE Hand.-Mazz. Sitzganz. Akad. Wiss. Wien. Math. Nat. 61: 23, 1924; Symb. Sin. 7: 1182, 1936). Type species, *D. amoena* (Hand.-Mazz.) Stebbins.

ARTIFICIAL KEY TO THE SPECIES OF DUBYAEA

A. Stems 1–7 dm tall, leafy (except sometimes in no. 7); involucres broadly campanulate, 20–80-flowered.
  B. Plants hirsute or glabrous; basal leaves relatively large, mostly 15–30 cm long and 2–8 cm broad, dentate or pinnatifid.
    C. Flowers blackish purple, dull brownish yellow, or bluish; achenes not at all rostrate; pappus setae yellow or tawny.
      D. Plants glandular-hispid; leaves lyrate-pinnatifid with a large terminal lobe; flowers blackish purple or dull brownish yellow; achenes 6.5–8 mm long . . 1. *D. atropurpurea*
      D. Plants glabrous and glaucous; leaves sinuate-pinnatifid; flowers purple or bluish purple; achenes about 3.5 mm long . . . . . 2. *D. glaucescens*
    C. Flowers bright yellow, orange yellow, or pinkish crimson; achenes more or less rostrate or subrostrate; pappus setae white or cream colored.
      E. Heads nodding; cuter involucral bracts relatively few; body of achene dark (at least in no. 4).
        F. Basal and lower cauline leaves on distinct, slender petioles; flowers pinkish crimson . . . . . 3. *D. rubra*
        F. Basal and lower cauline leaves sessile or cordate-clasping; flowers yellow . . . . . 4. *D. hispida*
      E. Heads erect; involucral bracts numerous and evenly imbricated; achenes stramineous throughout . . . . . 5. *D. oligocephala*

B. Plants completely glabrous; basal leaves smaller, 4–16 cm long and 0.6–2.2 cm broad, the margins entire.

G. Stems 2–4.5 dm tall; lower cauline leaves as large as the basal; heads 2–6 in an inflorescence; involucres 22–30 mm long; achenes 8.5–10 mm long, with a short, thick beak.....6. *D. chimiliensis*

G. Stems 0.9–2 dm tall, cauline leaves all reduced, mostly linear and bract like; heads solitary or rarely 2; involucres 12–16 mm long; achenes 4–5.5 mm long, not beaked.....7. *D. tsarongensis*

A. Plants acaulescent, the flowering scapes 1.5–7 cm long, naked or with a few linear bracts; involucres narrowly cylindric, 10–17-flowered.

H. Plants more or less glandular-hispid; leaves mostly pinnatifid; scapes 3–6.....8. *D. amoena*

H. Plants glabrous throughout; leaves entire or remotely and minutely denticulate; scapes solitary.....9. *D. gombalana*

SECTION I. EUDUBYAEA

1. DUBYAEA ATROPURPUREA (Franch.) Stebbins, Jour. Bot. 75 (1937): 51. (Fig. 2, *a–d*).

Perennial from a stout taproot; stems 3–7 dm tall, stout, angulate or striate, hirsute, leaves mostly cauline, the lower large, lyrate-pinnatifid, sessile, the blade glabrous above, sparsely short hirsute along the veins below; upper leaves elliptic, sinuate-dentate, usually cordate-clasping at the base; heads 3–8, nodding on elongate, densely blackish-hirsute peduncles; involucres large, broadly campanulate, about 60–70-flowered, 18–22 mm long, the bracts in several series, the outer narrowly lanceolate or linear, attenuate at the apex, the inner broadly lanceolate, 4–5.5 mm broad, all lead-color and blackish-hirsute at least along the midrib; corollas blackish violet, brown, or deep dull yellow, 15–18 mm long, the tube 3.5–4.5 mm long, $\frac{1}{5}$–$\frac{1}{3}$ as long as the ligule; anthers yellowish, 4–5.5 mm long; stigmatic branches 1.7–2.5 mm long, 0.3 mm broad; achenes 6.5–8 mm long, stramineous, oblong or somewhat fusiform, with about 10 strong ribs, and a few indistinct ones between them; pappus bristles 1–2-seriate, coarse, yellowish or rufescent, 8–10 mm long. (*Lactuca atropurpurea* Franch. in Morot, Journ. de Bot. 9: 294, 1895.)

Southwestern China and adjacent Burma, in subalpine and alpine meadows at 3000–4000 m. The following are typical:

CHINA: Yunnan Prov., eastern slopes of Lichiang Range, alt. 3640 m, *Forrest 6218* (E,B), *Rock 5373* (B,US); Tali Range, alt. 3330–3640 m, *Forrest 4060* (E); western flank of Shweli-Salween divide, alt. 3030 m, *Forrest 9025* (E); Tsangshan Range, *Rock 6349* (B); Mt. Habashan, *Rock 9707* (B); Fuchuan Range, alt. 3790 m, *Rock 23290* (UC); west of Hsiao-Chung-tien, *Rock 24626* (UC); Pi-lo-shan, Che-tse-lo, alt. 4000 m, *Tsai 58629* (UC, G). BURMA: Northeast upper Burma, N'Maikha-Salween divide, *Forrest 27299* (US,K).

This is unquestionably the most primitive species of *Dubyaea*. Its nearest relationship is with *D. hispida*, but the two species are nevertheless

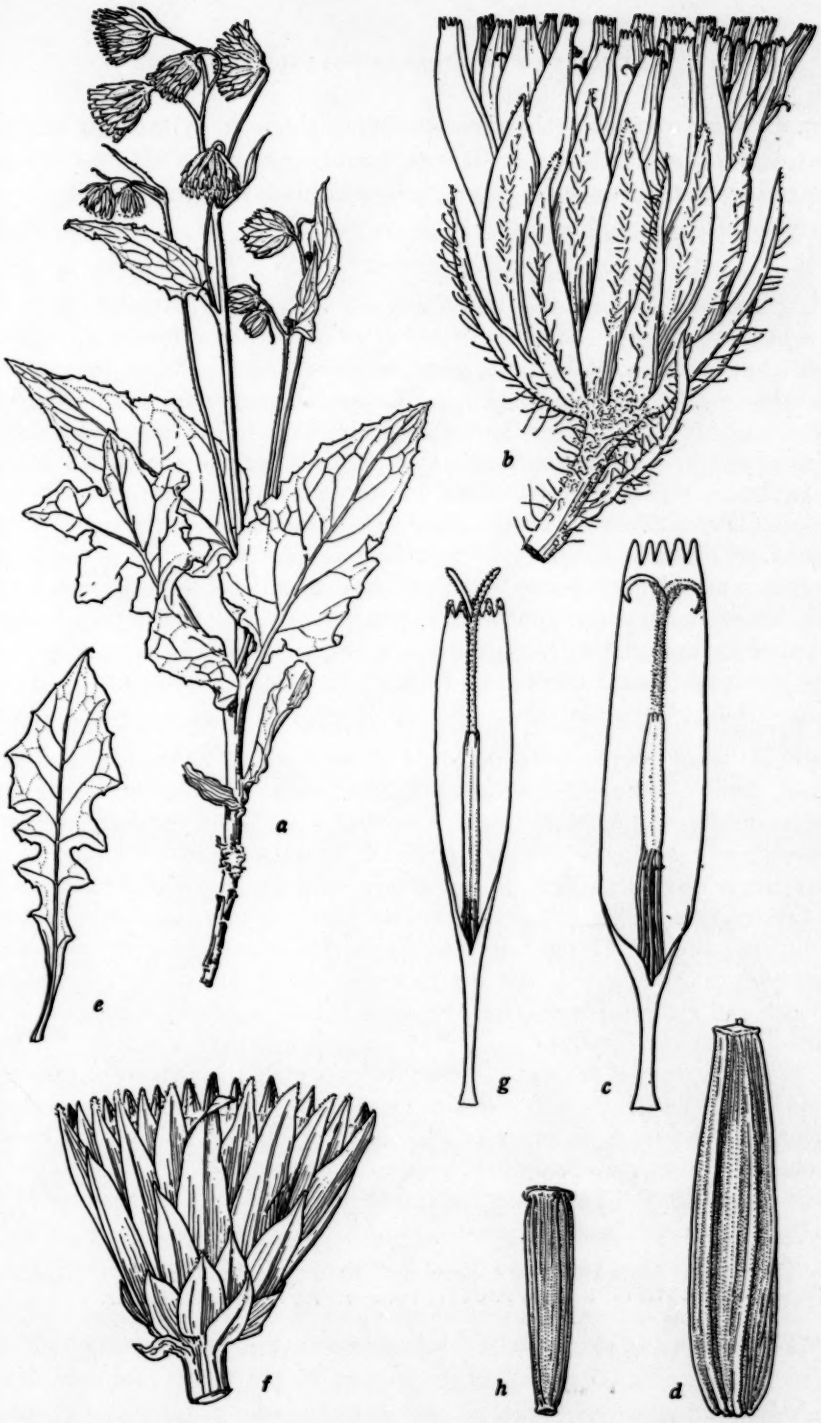

Fig. 2. *a–d. Dubyaea atropurpurea; a–c,* from *Rock 24626* (UC), *d,* from *Forrest 9025* (E); *a,* habit ×¼; *b,* involucre, ×2; *c,* corolla, ×4; *d,* achene, ×8. *e–h, D. glaucescens,* from cotypes (B, K); *e,* leaf, ×¼; *f,* involucre, ×2; *g,* corolla, ×4; *h,* achene, ×8.

very distinct from each other in a number of characteristics. Judging from the number of collections seen, it must be rather common within its range. The nomenclatural problem connected with this species has been discussed elsewhere (Stebbins, loc. cit.).

2. **Dubyaea glaucescens** sp. nov. (Fig. 2, *e–h*).—Caulis 40–50 cm altus, striatus, glaber; folia basalia sessilia anguste obovata, ca. 20 cm longa, 6 cm lata, sinuato-dentata vel pinnatifida, apice acuta vel acuminata, margine remote denticulata, glaberrima, glaucescentia, subtus pallida; folia caulina inferiora basalibus similia, basi amplexicaulia; folia superiora minora, elliptica vel ovata, cordato-amplexicaulia; capitula 3–4, longissime pedunculata, cernua, pedunculis 8–17 cm longis glaberrimis striatis; involucra 18–20 mm longa, late campanulata, multiflora, phyllis imbricatis glaberrimis, exterioribus deltoideis vel ovatis, acutsi, interioribus lanceolatis acutis, corollae purpureae (ex nota collectoris), 17 mm longae; antherae pallidae, 6–6.5 mm longae; rami stigmati 2 mm longi, pallidi; achaenia oblonga, 3.5 mm longa, apice truncata vel paullo contracta, inaequaliter ca. 12-costata, pallide fusca; pappi setae uniseriatae, sordide flavescentes, rigidae, 9–10 mm longae; receptaculum profunde foveolatum; foveolis margine valde erosis.

Perennial from a taproot, glabrous throughout; stem 40–50 cm tall, striate, glabrous; basal leaves sessile, narrowly obovate, about 20 cm long and 6 cm broad, sinuate-dentate or shallowly pinnatifid, acute or acuminate at the apex, the margin remotely denticulate, completely glabrous, glaucescent, paler below; lower cauline leaves similar to the basal, auriculate-clasping at the base, upper leaves smaller elliptic or ovate, cordate-clasping at the base; heads 3–4 per plant, nodding, solitary on the ends of elongate, stout, striate, glabrous peduncles, these 8–17 cm long; involucres 18–20 mm long, broadly campanulate, many-flowered, the bracts rather evenly imbricated, completely smooth and glabrous, lead-color, the outer deltoid or ovate, acute, the inner lanceolate, acute; corollas "purple" (collector's note), 17 mm long, the tube 5 mm, the ligule 12 mm long; anthers pale, yellowish or bluish, 6–6.5 mm long; branches of the stigma about 2 mm long and 0.2 mm broad, pale; achenes oblong, 3.5 mm long, truncate or slightly contracted at the apex, unequally about 12-costate, pale brownish; pappus bristles uniseriate, dull yellowish, coarse and stiff, 9–10 mm long; receptacle deeply pitted, the margins of the pits strongly erose.

Known only from the type collection: CHINA: Szechuan Prov., Omei Hsien, cliff, alt. 910–1210 m, *Wilson 2493* (G type, B, K, US).

This species is closest to *D. atropurpurea*, but is strikingly different from it, as well as from all other species of the genus. Its completely glabrous and glaucous habit, as well as its broad outer involucral bracts, set it off sharply from any other species of this section, and recall *D. tsarongensis* of the section *Ixeridopsis*. *D. glaucescens*, however, is totally

different from *D. tsarongensis* in other respects. The oblong, almost columnar achenes and yellow, uniseriate pappus of *D. glaucescens* suggest those of *Prenanthes* subg. *Nabalus* and *Hieracium*, but it does not approach these genera in other respects. The pollen grains are very large, 38–40μ in diameter, and are nearly all 4-pored. Since all species of Cichorieae with 4-pored pollen grains of which the chromosome number is known are cytologically polyploids, this suggests that *D. glaucescens* is also a polyploid.

The habitat of *D. glaucescens* differs from that of all other species of *Dubyaea*, since it occurs at low altitudes, in a zone characterized by a warm temperate climate and by the presence of a mixed deciduous forest containing a great wealth of genera and species of woody plants.

3. **Dubyaea rubra** sp. nov. (Fig. 3, *e–f*)—Herba perennis; caulis 4.5–6 dm altus, ad basim glaber, ad apicem hirsutus pilis glandulosis; folia basalia petiolata, sagittata, 3.5–7 cm longa, 2.5–4.5 cm lata, margine remote denticulata vel dentata; folia caulina elliptica, inferiora petiolata, superiora sessilia, nec cordata nec amplexicaulia; capitula 4–6 pro planta, longe pedunculata, cernua, multiflora; involucra 15–17 mm longa, phyllis imbricatis, linearis vel lanceolatis, dense nigro-hirsutis, acutis vel acuminatis; corollae roseo-rubescentes, 17–18 mm longae; antherae 5 mm longae, nigrescentae; achaenia ignota; pappi setae multiseriatae, albae vel lacteae, 9–10 mm longae.

Perennial herb; stem 4.5–6 dm high, glabrous toward the base, hirsute toward the apex with glandular hairs; basal leaves petiolate, sagittate, 3.5–7 cm long, 2.5–4.5 cm broad, remotely denticulate or dentate on the margin; cauline leaves elliptic, acute, the lower petioled, the upper sessile but not cordate-clasping; heads 4–6 in a corymbose inflorescence, nodding on elongate peduncles; involucres campanulate, about 50–60-flowered, 15–17 mm long, the bracts inbricated in several series, the outer shorter, all linear or lanceolate, densely blackish-hirsute, acute or acuminate; corollas "pinkish crimson" (collector's note), 18–19 mm long, the tube 8 mm, the ligule 10–11 mm long, 1.8–2 mm broad; anthers 5 mm long, greenish or blackish; branches of the stigma 1.8–2 mm long; pappus setae multiseriate, white or cream color, 9–10 long; achenes not seen.

Known only from the type. CHINA: Szechuan Prov., Muli, alt. 3940 m, *Ward 4836* (E).

This species is very close to *D. hispida*, from which it differs chiefly in the shape of its basal leaves, the lower cauline leaves petioled, the upper cauline leaves not at all cordate-clasping, and in its smaller, pinkish-crimson corollas and dark anther tubes. It is taller than most of the *D. hispida* seen from China, but is equalled in height by specimens of that species from the western Himalaya.

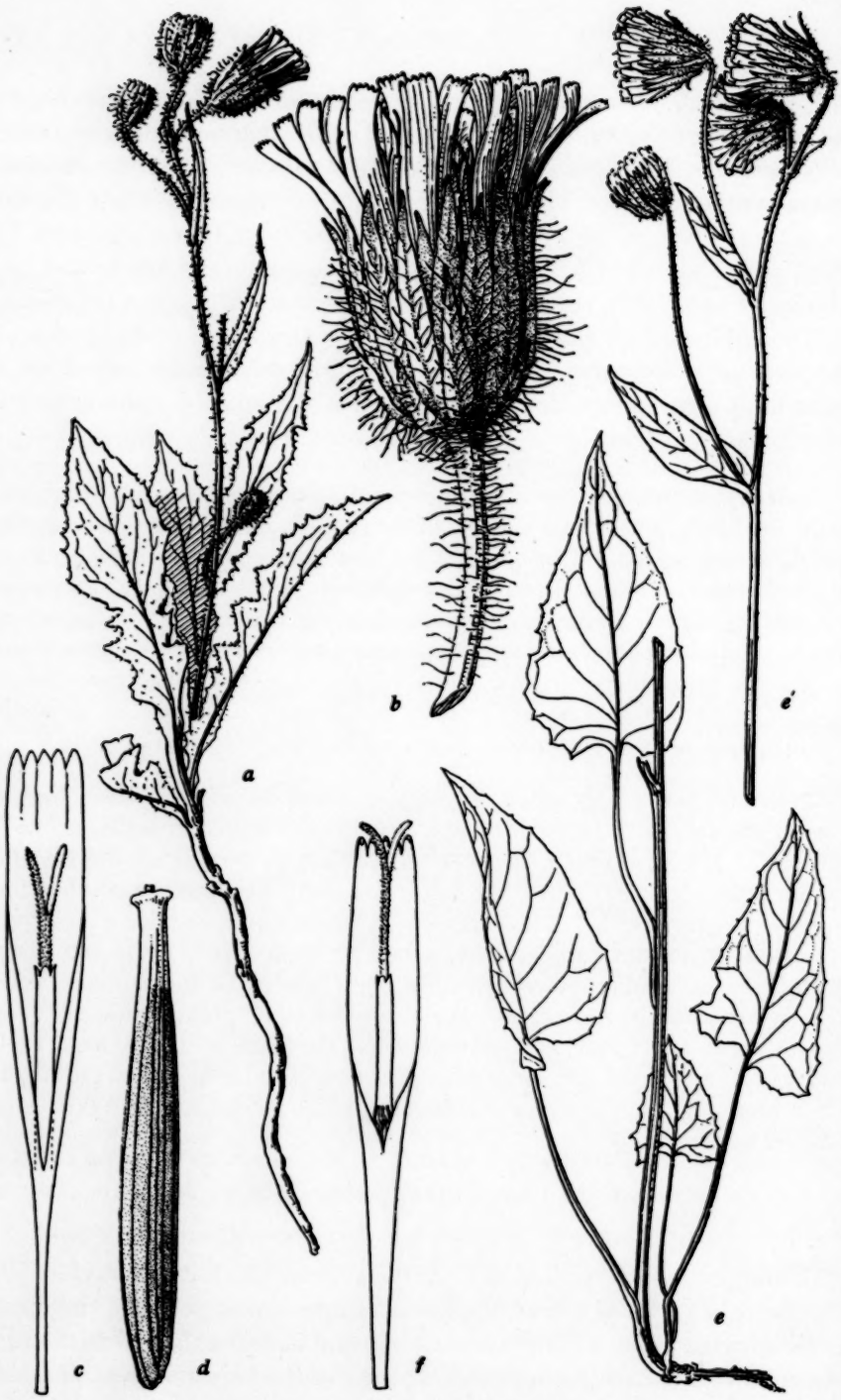

Fig. 3. *a–d, Dubyaea hispida;* *a–b* from *Handel-Mazzetti 9988* (UC), *c,* from *Bees 3533* (K), *d,* from *Hort. Calif. Genet. 3245;* *a,* habit, ×½; *b,* involucre, ×2; *c,* corolla, ×4; *d,* achene, ×8. *e–f Dubyaea rubra,* from type (E); *e,* habit, ×½; *f,* corolla, ×4.

4. DUBYAEA HISPIDA (Don) DC., Prod. 7: 247, 1838. (Fig. 3, *a–d*)—Stems from a creeping rhizome, 1.2–6 dm tall; basal leaves sinuate-dentate to lyrate-pinnatifid, the blade sparsely brownish-hirsute on both surfaces or glabrate above; cauline leaves 2–8, the lower similar to the basal, the upper gradually reduced, elliptic or ovate, mostly cordate-clasping at the base; heads 2–16 in a corymbose inflorescence, nodding, on elongate, blackish-hirsute peduncles; involucres campanulate, 15–20 mm long, the outer bracts acute or acuminate, narrowly lanceolate or the outermost linear, the longest $\frac{2}{3}$–$\frac{4}{5}$ the length of the inner; inner bracts about 18–20, lanceolate, acute, 2–3 mm broad, blackish-hirsute at least along the midrib; florets about 40–50 per involucre; corollas yellow, 20–25 mm long, the tube glabrous, 6–10 mm long, shorter than the ligule; anthers yellow, 4–5.5 mm long; stigmatic branches blackish, 2–2.5 mm long; achenes fusiform, somewhat obcompressed, 6.5–9 mm long, the body brownish or blackish, the apex pale, stramineous, subrostrate; pappus setae multiseriate, cream color, 10–12 mm long. (*Hieracium hispidum* Don, Prod. Fl. Nepal, 165, 1825, non Forsk.; *H. heteranthum* Wall. cat. n. 3253; *Lactuca Dubyaea* C. B. Clarke, Comp. Ind. 271, 1876; Hook. f., Fl. Brit. Ind. 3: 409, 1882; *Crepis bhotanica* Hutchinson, Kew Bull. 1916: 189; *Crepis Dubyaea* Marq. et Shaw, Jour. Linn. Soc. 48: 194, 1929.)

Western Himalaya in Kumaon and Garwhal Provinces, east to western China, Szechuan Province, in meadows or open alpine slopes at 3000–4500 m altitude. The following, selected from a considerable series, are tyical: INDIA: Kumaon Province, near Ralaim, alt. 3330–3635 m, *Duthie 3093* (B, DD); Sikkim Prov., Megu, alt. 4090 m, *Ghose* in 1932 (UC). BHUTAN: without locality, *Bees 3533* (type of *C. bhotanica* Hutchinson, K). BURMA: Semhku Valley, alt. 3330–3635 m, *Ward 7538* (K). TIBET: Tomo La, alt. 4240 m, *Ward 6188* (K). CHINA: Yunnan Prov., Mekong-Salwin divide, alt. 4240 m, *Forrest 20730* (B, K); Szechuan Prov., Mt. Konka, alt. 4480 m, *Rock 16883* (B).

This is much the most widespread and best known of the species of *Dubyaea*. It is remarkably uniform throughout its range, the variation found being chiefly in the height and luxuriance of the plant, and to a lesser extent the shape of the leaves. The chromosome number has been already reported as $2n = 16$ (Babcock, Stebbins and Jenkins 1937).

5. DUBYAEA OLIGOCEPHALA (Sch. Bip.) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 4)—Stems from a taproot, 1.5–4.5 dm tall, hirsute or nearly glabrous below, glabrous or hirsute above; basal leaves oblanceolate to obovate in outline, lyrate pinnatifid or merely dentate, the apex acuminate, glabrous or pubescent; cauline leaves 2–6, the lowermost similar to the basal, the upper reduced, lanceolate, cordate-clasping at the base; heads 2–6 in a cymose inflorescence, erect on divergent peduncles 2–14 cm long; involucres campanulate, 14–20 mm long, the bracts numerous, evenly imbricated in several series, narrowly deltoid to lanceolate, obtuse or somewhat acute at the apex, glabrous or tomentulose on the outer surface, the outer ones strongly ciliate along the margins; florets about 70–80 per involucre; corollas yellow, 18–25 mm long,

the tube glabrous, shorter than the ligule; anthers yellow, 4.5–5.5 mm long; stigmatic branches blackish, 2.5–3 mm long; achenes stramineous, fusiform, somewhat obcompressed, total length 7–12 mm tapering upward into a stout beak $\frac{1}{5}$–$\frac{1}{3}$ as long as the body, unequally about 12-ribbed; pappus setae white, less coarse than other species of *Dubyaea*, 7–9 mm long, more or less deciduous at maturity. (*Crepis sibirica* Clarke, Comp. Ind.: 252, 1876; Hook. f., Fl. Brit. Ind. III: 394, 1882, *non* L.)

Western Himalaya Mountains, in Kashmir and adjacent Punjab, in open, rocky or gravelly places at altitudes of 2230–3000 m.

Clarke, (loc. cit.) identified this species with the northern Asiatic *Crepis sibirica* L., which it resembles superficially. *D. oligocephala*, however, has the involucral bracts much more numerous and evenly imbricated than *C. sibirica;* its stigmatic branches are blackish and somewhat flattened, as in other species of *Dubyaea*, while those of *C. sibirica* are yellow, more slender, and nearly terete, as is typical of *Crepis;* and finally D. *oligocephala* has the obcompressed, unequally ribbed achenes of *Dubyaea*, while those of *C. sibirica* are typical of *Crepis* in being terete and equally ribbed. Hooker (loc. cit.) noted that the achenes of the specimens of "*Crepis sibirica*" (*D. oligocephala*) seen by him were "quite smooth," and added the comment: "I have *not* quoted Boisser who describes the achenes (of *C. sibirica*) as 20–30-ribbed, the ribs transversely rugulose and scaberulous." Boissier described the achenes of true *C. sibirica* quite correctly, while Hooker's description is equally correct for *D. oligocephala*. Apparently neither Hooker nor Clarke compared mature achenes of the Indian plant with those of true *Crepis sibirica*.

Dubyaea oligocephala occupies the western limit of the range of the genus. It is most closely related to *D. hispida*, which it also approaches geographically. There is, however, a gap of about 240 km (150 miles) in the western Himalaya between the known ranges of *D. hispida* and *D. oligocephala*, in which area no species of *Dubyaea* is known to occur. *D. oligocephala*, moreover, occupies a somewhat different habitat from that of *D. hispida*, occurring at lower elevations, and apparently in drier situations.

Two subspecies of *D. oligocephala* may be recognized, and are distinguished as follows:

Basal leaves 1.5–5 cm broad; broadest involucral bracts 3–4 mm broad, outermost bracts not usually squarrose; mature achenes 9–12 mm long.....a. *typica*

Basal leaves 4.5–8 cm broad; broadest involucral bracts 2.2–2.8 mm broad, the outer ones squarrose; mature achenes 7–8.5 mm long.....b. *latifolia*

5a. **Dubyaea oligocephala typica** nom. nov. (Fig. 4, *a–f*)—Basal leaves lanceolate, 12–28 cm long, 1.5–5 cm broad, their lobes deltoid, acute at the

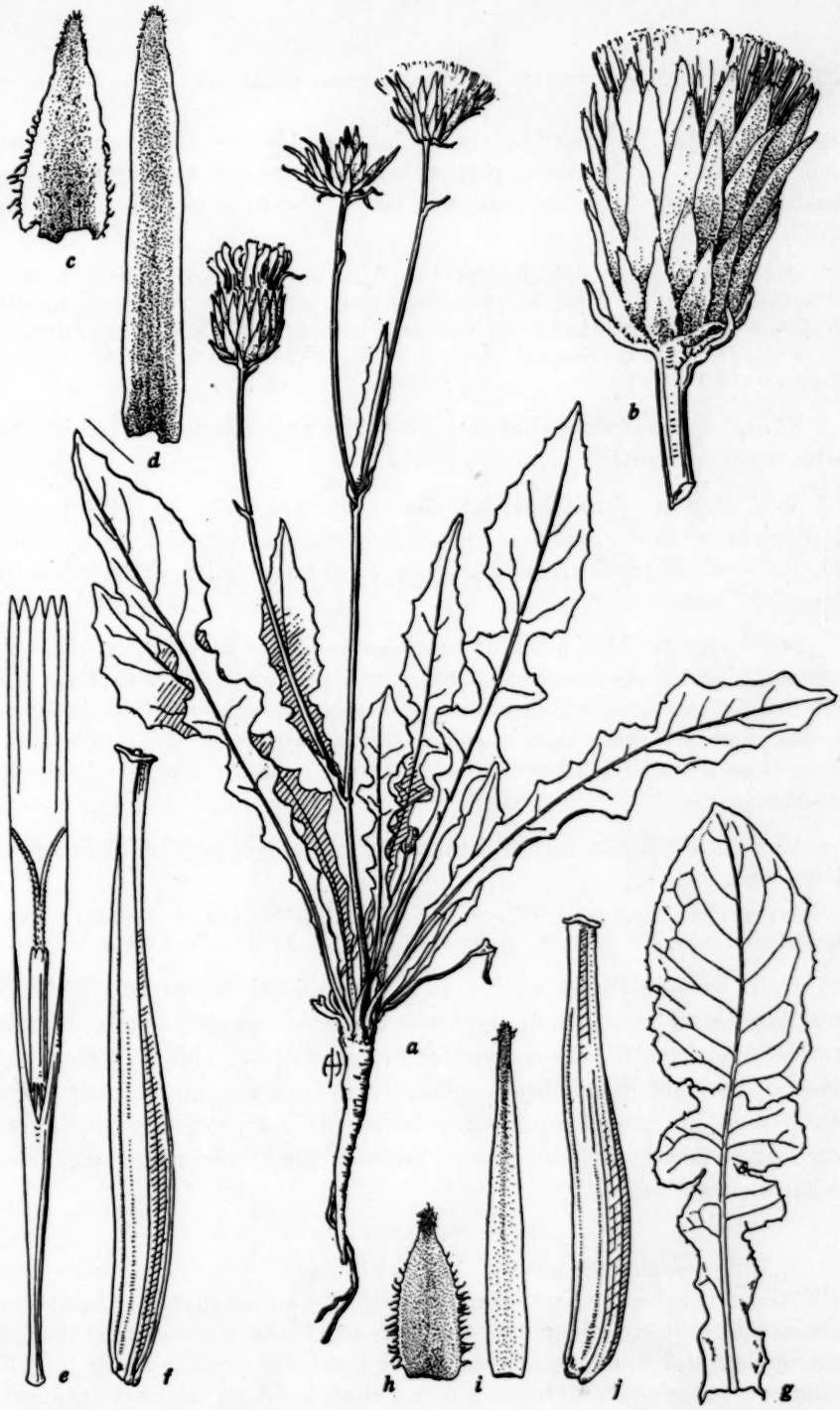

Fig. 4. *Dubyaea oligocephala*. *a–f*, subsp. *typica; a, c, d*, from type and cotype; *b, e*, from *Clarke 31335* (Calcutta); *f*, from *Stewart 12381* (UC). *a*, habit, ×½; *b*, involucre, ×2; *c, d*, outer and inner involucral bracts, ×4; *e*, corolla, ×4; *f*, achene, ×8. *g–j*, subsp. *latifolia*, from type (K); *g*, leaf, ×½; *h, i*, involucral bracts, ×4; *j*, achene, ×8.

apex; plants hispid or nearly glabrous; involucral bracts rather broad, mostly 2–4 mm broad at the widest part; achenes slender and with well developed beaks, 9–12 mm long, including the beak. (*Paleya oligocephala* Sch. Bip., Pollichia 2: 320, 1866.)

The following are typical: INDIA: Kashmir Prov. without definite locality, *Jacquemont 1205* (P type, K, photo and fragments in UC); without locality, *Falconer 613* (K); Marbul Pass, 3030 m, *Clarke 31335D* (K); Laka, *Edgeworth 5048* (K); Sonamarg, *Stewart 12381* (UC, K, NY, G); Punjab Prov., Murree, *Saunders* in 1914 (K).

Subsp. *typica* is somewhat variable in size and pubescence, but is otherwise very constant.

5b. **Dubyaea oligocephala latifolia** subsp. nov. (Fig. 4, *g–j*)—A subsp. typica differt foliis latioribus, 4.5–8 cm latis; segmentis obtusis vel rotundatis; phyllis involucri pluribus, angustioribus, 1.2–2.8 mm latis; achaeniis brevioribus, 7–8.5 mm longis.

Stems densely hispid below; basal leaves short-pubescent on the upper surface, hispid along the veins below, narrowly obovate, 14–28 cm long, 4.5–8 cm broad, the apex acute or obtuse, the lobes obtuse or rounded; involucral bracts more numerous than in subsp. *typica*, narrow, 1.2–2.8 mm broad (at least in each head 2.2–2.8 mm broad); achenes 7–8.5 mm long, the beak often nearly absent.

Western Himalaya, east of the range of subsp. *typica*. The following have been seen:

INDIA: Punjab Prov., Dharmsala, alt. 2730 m, *Clarke 24012* (K *type*); near Dalhousie, alt. 2270 m, *Drummond 983* (K); Dalhousie, *Clarke 22439* (K).

In its broader leaves, as well as in its hispid character, relatively narrow involucral bracts, and shorter achenes, subsp. *latifolia* is somewhat transitional from *D. oligocephala* toward *D. hispida*. This is interesting in view of the fact that subsp. *latifolia* occupies a range adjoining that of *D. hispida*, and about equidistant between the known western limits of the latter species, and the eastern limits of the known range of *D. oligocephala* subsp. *typica*.

SECTION 2. IXERIDOPSIS

6. **Dubyaea chimiliensis** (W. W. Smith) comb. nov. (Fig. 5, *a–c*)—Plant glabrous throughout; stems from a taproot, 2–4.5 dm tall; larger basal leaves oblanceolate, 8–18 cm long, 1.5–2.2 cm broad, obtuse or apiculate at the apex; cauline leaves 2–4, sessile, similar to the basal, the lower 6–14 cm long, the upper gradually reduced; heads 2–6 on a stem, nodding, on slender peduncles, the lower of which arise from the upper leaves; involucres 22–30 mm long, broadly campanulate, about 30–35-flowered, the bracts oblanceolate to narrowly elliptic, acute, loosely imbricated, 5–8 mm broad at the widest part;

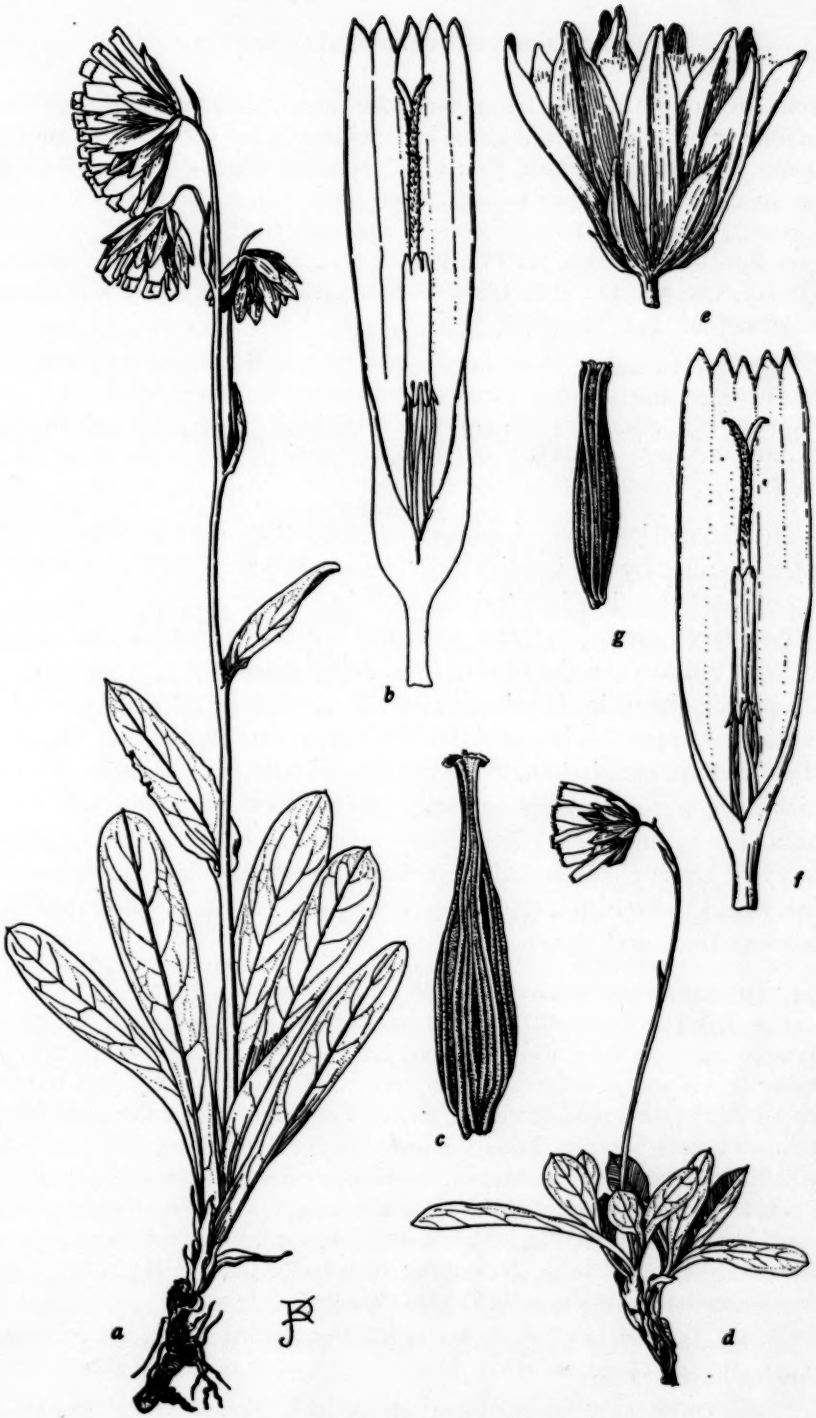

Fig. 5. *a–c*, *Dubyaea chimiliensis*, from *Forrest 25021* (US, E); *a*, habit, ×½; *b*, corolla, ×4; *c*, achene, ×8. *d–g*, *Dubyaea tsarongensis*, *d–f*, from cotype (E); *g*, from *Rock 22545* (UC); *d*, habit, ×½; *e*, involucre, ×2; *f*, corolla, ×4; *g*, achene, ×8.

corollas golden yellow, 18–23 mm long, the tube 3.5–4.5 mm, the ligule 15–18 mm long, sharply contracted at the base; anther tube yellow, 5.5–6 mm long; stigmatic branches blackish, flattened, 1.6–2 mm long; achenes 8.5–10 mm long, fusiform, tapering to a short, thick beak; pappus setae yellow, fragile, deciduous, 7.5–8.5 mm long. (*Lactuca tsarongensis* f. *chimiliensis* W. W. Smith, Notes Bot. Gard. Edinb. 12: 211, 1920; *Crepis tsarongensis* var. *chimiliensis* Anthony, op. cit. 18: 194, 1934; *Dubyaea tsarongensis* subsp. *chimiliensis* Stebbins, Jour. Bot. 75 (1937): 18.)

Chimili Mountains, Northeast Upper Burma, in alpine meadows. The following have been seen:

BURMA: west flank of Chimili, alt. 3330–4240 m, *Forrest 24936* (E, NY, US); *25021* (E, K, NY, US), *26947* (E, K, NY, US); *27254* (K); *27306* (K, B, US).

The recognition of *D. chimiliensis* as a species is, in the opinion of the writer, justified by the definite differences between it and *D. tsarongensis*, not only in habit, but in floral characteristics as well. The involucres of *D. chimiliensis* are much larger and their bracts are broader. The corollas are quite different in shape (Fig. 5b), being markedly contracted at the base of the ligule in *D. chimiliensis*. Furthermore, the achenes of *D. chimiliensis* appear to be considerably larger than are those of *D. tsarongensis*, and are definitely rostrate, while the only ones of *D. tsarongensis* which have been seen, although they are immature, do not look as if they would develop any beak. There is no overlapping between the two species in any of these characteristics. In fact, no intermediate forms between them would be expected, since they occupy different mountain ranges, 160 km apart from each other.

7. DUBYAEA TSARONGENSIS (W. W. Smith) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 5, *d–g*)—Plant with the general habit of *D. chimiliensis*, but smaller throughout; stems 0.9–2 dm tall; basal leaves 4–10 cm long, 6–15 mm broad; cauline leaves much reduced, often linear and bract-like; heads solitary or rarely 2 on the stem; involucres 12–16 mm long, about 20–25-flowered; broadest inner bracts 3–5 mm broad; corollas 18.5–22 mm long, the tube 3.5–5, the ligule 15–18 mm long, gradually tapering toward the base; anther tube 3.5–5.5 mm long; achenes (immature) 4–5.5 mm long, truncate or slightly tapering toward the apex, but not at all beaked; pappus setae 6–7 mm long. (*Lactuca tsarongensis* W. W. Smith, Notes Bot. Gard. Edinb. 12: 211, 1920; *Crepis tsarongensis* Anthony, op. cit. 18: 194, 1934.)

Southeastern Tibet and adjacent Upper Burma, in alpine meadows. The following have been seen:

TIBET: Doker-La, Tsarong Prov., alt. 3330 m, *Forrest 16871* (E *type*, K); Mt. Kenichunpo, north of Sikitung, alt. 4090 m, *Rock 22148*, *22545* (UC); UPPER BURMA: Imaro Bum, *Ward 3585* (E).

In habit, size of heads, and shape of achenes, *D. tsarongensis* is nearer to *D. amoena* and *D. gombalana* than to *D. chimiliensis*, which it is in other respects much more closely related. In fact, *D. chimiliensis* and *D. tsarongensis* are in a way connecting links between the sect. *Eudubyaea* and the sect. *Amoenae*.

SECTION 3. AMOENAE

8. DUBYAEA AMOENA (Hand.-Mazz) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 6, *a–c*)—Dwarf acaulescent perennial from a fusiform taproot; basal leaves 4–12 cm long, repand-dentate or pinnatifid, the lobes triangular-lanceolate, glabrous or sparingly glandular-hirsute on the midrib above; scapes 3–6, 2–7 cm long, glandular-hirsute, naked or with 1–2 linear bracts; involucres 15–18 mm long, narrowly campanulate, the bracts relatively few, evenly imbricated, lanceolate, blackish, glandular-hirsute; florets 10–16 per involucre; corollas blue or bluish purple, 20–27 mm long, the tube 6–9 mm long; anther tube blackish-blue (in sicc.), 3.5–4 mm long; mature achenes stramineous or somewhat reddish, 5.5–6.5 mm long, somewhat obcompressed, with 5 distinct nerves, otherwise smooth; papus setae 11–12 mm long, persistent, multiseriate, stiff and coarse, rufescent. (*Lactuca amoena* Hand.-Mazz., Sitzganz. Akad. Wiss. Wien. Math-Nat. 61: 23, 1924; Symb. Sin. 7: 1183, t. 17, fig. 12, 1936.)

Northwestern Yunnan and adjacent Tibet, in rocky alpine slopes and pastures. The following have been seen:

CHINA: Yunnan Prov., Salwin-Irrawady divide above Chamutong, alt. 3825 m, *Handel-Mazzetti 9913* (V *type*, B); TIBET: Tsarong Prov., Salwin-Kiu Chiang (Irrawady) divide, alt. 4390 m, Forrest *18889* (B), *20331* (B, US), *22936* (B, US); Mt. Kenichunpo, alt. 4090–4240 m, *Rock 21975*, *22518* (UC).

The stiff, coarse pappus bristles and flattened stigmatic branches as well as the shape and ribbing of the achenes, serve to place this species in *Dubyaea* rather than *Lactuca*. The mature achenes resemble those of *D. atropurpurea*, except that they have fewer ribs.

9. DUBYAEA GOMBALANA (Hand.-Mazz.) Stebbins, Jour. Bot. 75 (1937): 17. (Fig. 6, *d–e*)—In habit similar to *D. amoena;* basal leaves 3–9 cm long, narrowly lanceolate, acute or apiculate, entire or minutely and remotely denticulate; scapes solitary, 1.5–5 cm long, glabrous; involucres narrowly campanulate, 13–17 mm long, the bracts evenly imbricated, glabrous; florets 10–17, corollas about as in *D. amoena;* anther tube pale, 4–4.5 mm long; mature achenes not seen, but presumably like those of *D. amoena;* pappus setae as in *D. amoena*. (*Lactuca gombalana* Hand.-Mazz., Sitzganz. Akad. Wiss. Wien, Math-Nat. 61: 23, 1924; Symb. Sin. 7: 1183, t. 17, fig. 13, 1936.)

Northwestern Yunnan and adjacent Tibet. The following have been seen: YUNNAN: Mt. Gomba-la, Salwin-Irrawady divide above Chamutong, alt. 3900 m, *Handel-Mazzetti 9889* (V *type* B); TIBET: Tsarong Prov., Salwin-Kiu-

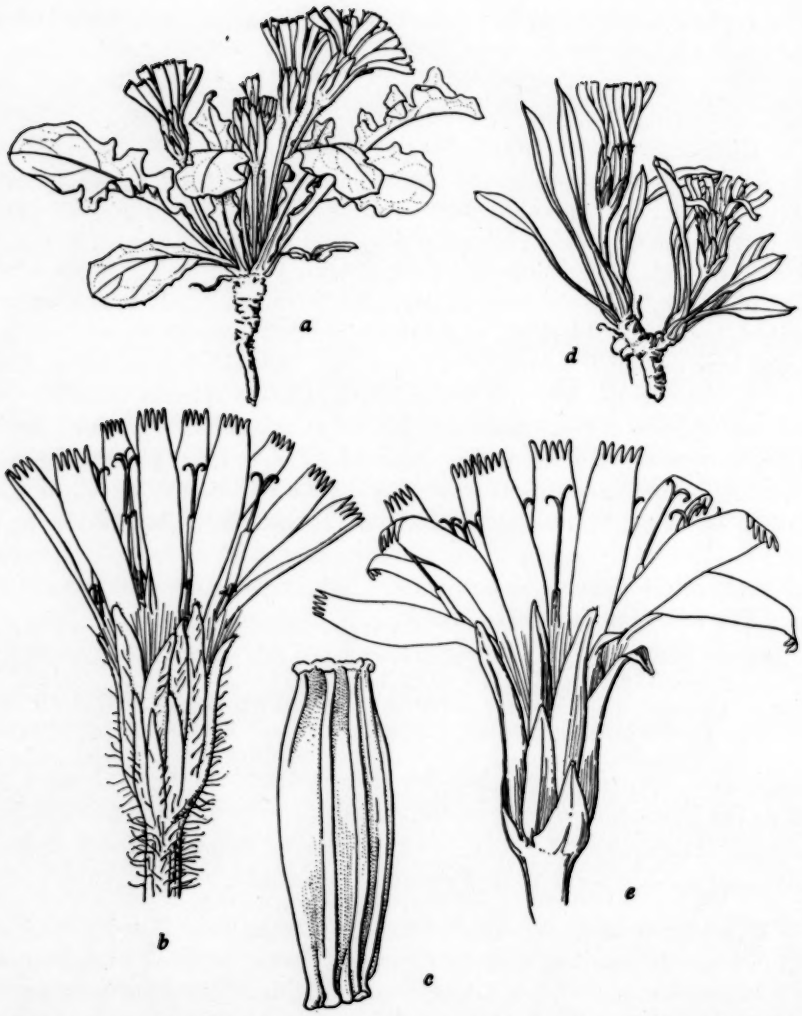

Fig. 6. *a–c, Dubyaea amoena, a–b,* from type (V); c, from *Rock 22518* (UC); *a,* habit, ×½; *b,* involucre, ×2; *c,* achene, ×8. *d–e Dubyaea gombalana,* from type (V); *d,* habit, ×½; *e,* involucre, ×2.

Chang divide, alt. 4240–4545 m, *Forrest 20257* (B, US); Mt. Kenichunpo, north of Sikitung, alt. 4240 m, *Rock 22160* (UC, US).

This species is close to *D. amoena*, but differs in its solitary scapes, the shape of its leaves, and in being glabrous throughout. In all of these respects it is transitional toward *D. tsarongensis*. The three species, *D. tsarongensis*, *D. amoena*, and *D. gombalana*, all found on the same mountain range and all except *D. tsarongensis* known only from this range, form the most striking case of endemism in the whole tribe of Cichorieae in Eastern Asia. They have no close relatives, except for the equally isolated *D. chimiliensis*, which occurs on a neighboring mountain range further south. The origin of these isolated endemics in post-Pleistocene time is difficult to imagine; they represent much more likely the last remnants of a group which was formerly more widespread.

SPECIES EXCLUSAE

Dubyaea cristulata DC., Prod. 7: 247. = Sonchus sp. (?)
Dubyaea ramosissima Hance ex Walp., Ann. 2: 1028 = *Ixeris denticulata* (Houtt.) Stebbins subsp. *ramosissima* (Benth.) Stebbins.
Dubyaea sonchoidea DC., Prod. 7: 247. = *Taraxacum montanum* DC.

IV. THE GENUS SOROSERIS

GENERIC DESCRIPTION

Soroseris, gen. nov. (Compositae-Cichorieae)—Herbae perennes pumilae laticiferae; caulis crassus, brevis, saepe cavus, ad basim saepissime cataphyllis ovatis vel lanceolatis vestitus, inflorescentia aggregata glomerata, capitulis numerosis, cymosa vel racemosa; flosculis 4–25 pro involucro; phylla involucri 2–3 seriata, extima 2 vel rarius 3–4, linearia, interiora subaequalia, lanceolata, ovata, vel anguste elliptica, ad basim coalescentia; corollae ligulatae, ligulis luteis vel albidis; antherae breviter caudatae, lutescentia vel nigrovirescentia; rami stigmati nigrescentes vel virescentes, leviter compressi, 1–3.5 mm longi, 0.2–0.35 mm lati; achaenia oblonga ad basim attenuata, ad apicem parce vel abrupte contracta, leviter obcompressa, multistriata; pappus setosus, setis simplicibus, numerosissimis, multiseriatis, crassis, rigidis, maturitate deciduis; receptaculum concavum, nec ciliatum nec paleaceum.

Dwarf alpine perennials with milky juice; stems thick, often hollow, usually short and partly or wholly subterranean: lowermost leaves usually replaced by bladeless petiolar cataphylls; upper leaves various; aggregate inflorescence glomerate, the heads numerous and closely crowded, cymose or somewhat racemose; involucres 4–25-flowered; involucral bracts in 2–3 series, the outermost usually 2, sometimes 3 or 4, narrowly linear, shorter than or exceeding the inner ones; inner bracts subequal, lanceolate, ovate, or narrowly elliptic, somewhat coalescent at the base; flowers perfect, bisexual; corollas ligulate,

yellow or white, often blackish at the base of the ligule; anthers shortly caudate, yellowish, greenish, or blackish; pollen grains subechinolophate or merely echinate, the spines large; stigmatic branches blackish or greenish, somewhat flattened, 1–3.5 mm long, 0.2–0.3 mm broad, the barbs on their outer surface numerous, acute, deltoid in outline, those on the style below the stigma few, not enlarged; achenes oblong, somewhat attenuate at the base and slightly but abruptly contracted at the apex; slightly obcompressed, convex on the outer, angulate on the inner surface, many striate; pappus setose, the setae very numerous, multiseriate, simple, coarse and stiff, deciduous from the mature achene; receptacle concave, slightly pitted, not paleaceous or fibrillate. Type species: *Soroseris glomerata* (Decne.), = *Prenanthes glomerata* Decne. Basic chromosome number, x = 8. The generic name is compounded from the two Greek words σωρός, a heap, and σέρις, an ancient name for a Cichoriaceous plant. It refers to the unusual habit of these plants.

RELATIONSHIPS OF SOROSERIS

In most of its floral characteristics, that is the character of the corollas, style and stigmas, the pappus, and the vascular anatomy of the florets, *Soroseris* is similar to *Dubyaea*, *Youngia* Sect. *Desiphylum*, and *Prenanthes*, subg. *Nabalus*. The bulk of its species, however, those belonging to the section EUSOROSERIS, are strikingly different from any of these three groups in the following characteristics. Their habit is quite different from that of any of these groups, but is approached by *Dubyaea* Sect. AMOENAE and by *Youngia* Sect. DESIPHYLUM. The sections of *Lactuca* and *Crepis* which approach *Soroseris* in habit are very different from it in floral characteristics, as will be explained below. The other distinctive characteristics possessed by Sect. EUSOROSERIS are the pair of elongate, linear outer involucral bracts, the predominance, except in *S. glomerata*, of four inner bracts and four florets per involucre (in *Prenanthes*, *Youngia*, and most other Cichoriaceous genera the number of florets, when greatly reduced, is usually 5 rather than 4); the concave receptacle with the involucral bracts more or less coalescent at the base; and the character of the styles and pollen grains. The styles of Sect. EUSOROSERIS are distinctive in having very few barbs below the forking of the stigmatic branches: they lack the "collecting hairs" so characteristic of most genera of the Cichorieae (Figure 7, b–c). The pollen grains of this section differ from those of most genera of the Cichorieae in being merely echinate, without a trace of the ridged or lophate pattern (Figure 7, d–g, compare Wodehouse 1928, 1935). The only species known among the relatives of *Soroseris* which has these distinctive types of stigma and pollen grain is *Pernanthes subpeltata* Stebbins, an isolated species of Africa, which is very different in habit and in other respects from *Soroseris* (Stebbins 1937c).

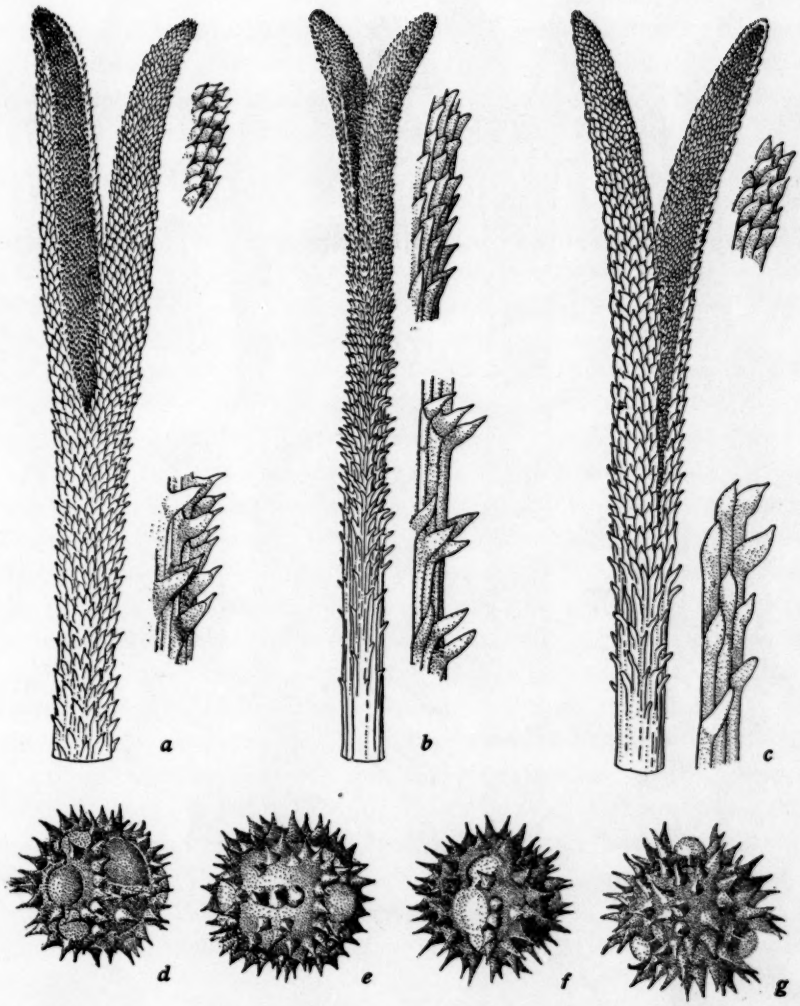

Fig. 7. *a–c*, stigmas of *a*, *Dubyaea atropurpurea*, *b*, *Soroseris umbrella*, *c*, *Soroseris glomerata*. Whole stigmas, ×25; detail of surface ×100. *d–g*, pollen grains, ×000, of *d*, *Dubyaea atropurpurea*, oblique poral view; *e*, *Soroseris umbrella*, equatorial view; *f*, *g*, *Soroseris glomerata*, *f*, oblique poral, *g*, polar view.

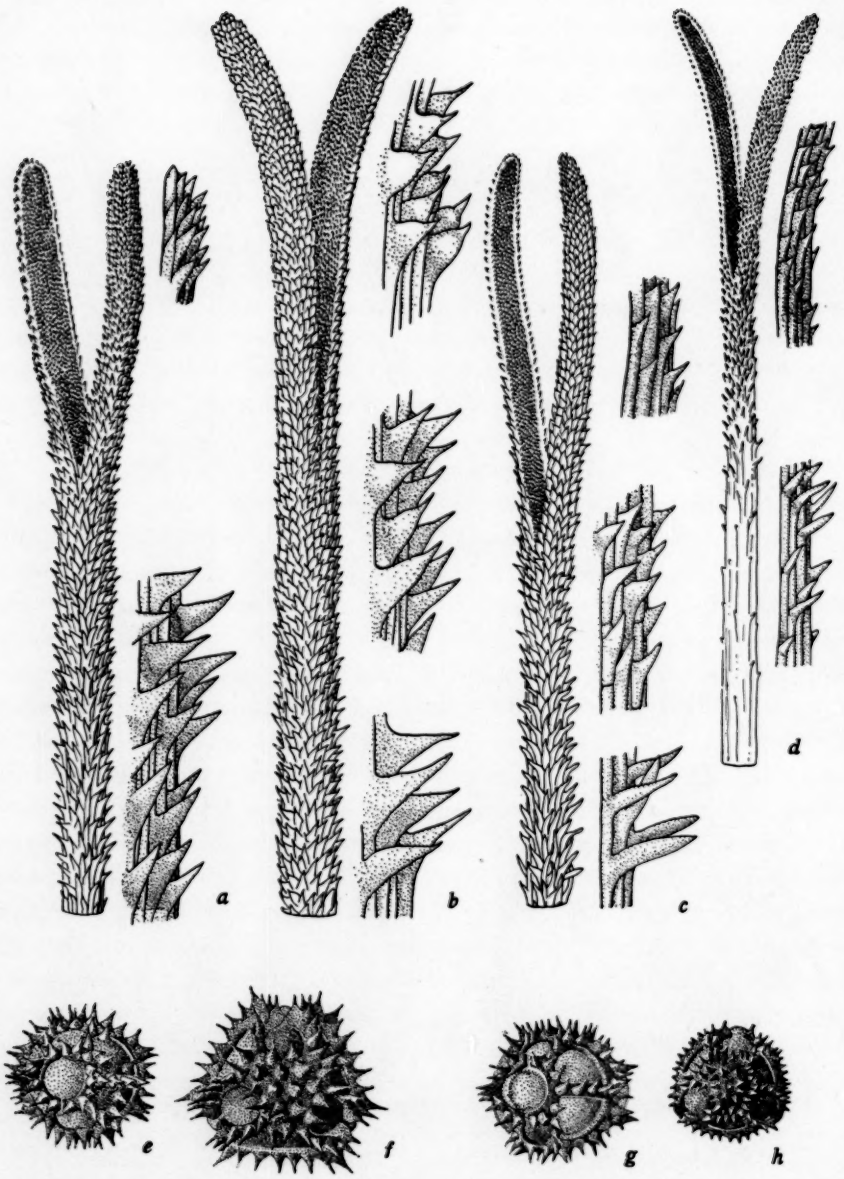

Fig. 8. *a–d* stigmas of *a*, *Prenanthes trifoliolata* (Cass.) Fernald, *b*, *Lactuca atropurpurea* Franch., *c*, *Crepis sibirica* L., *d*, *Crepis tectorum* L. *e–h*, pollen grains of *e*, *Prenanthes trifoliolata*, oblique poral view; *f*, *Lactuca atropurpurea*, polar view; *g*, *Crepis sibirica*, oblique poral view; *h*, *Crepis tectorum*, polar view. Magnification as in Fig. 7.

If the Sect. EUSOROSERIS were the only section of *Soroseris* extant, the genus would be a very much isolated one, whose affinities would be obscure. *S. umbrella*, however, of the Sect. DUBYAEOPSIS, is definitely a connecting link toward the genus *Dubyaea*. *S. umbrella* has the habit, the linear outer bracts, the concave receptacle, and coalescent inner bracts, the achene shape and the deciduous pappus setae characteristic of *Soroseris*, but in its large heads with numerous involucral bracts and florets, it resembles *Dubyaea*. Its styles and pollen grains are intermediate between these of Sect. EUSOROSERIS and those of *Dubyaea* (Fig. 7). There is another, but less obvious relationship between Sect. EUSOROSERIS and *Dubyaea* Sect. AMOENAE. The habit of these two sections is somewhat similar. Sect. EUSOROSERIS differs chiefly in having much more numerous and shorter peduncles. There is also some similarity between *S. Gillii* and *D. amoena* in leaf shape. The involucres, florets, and achenes of the two sections are. however, very different from each other. The glabrous habit and the leaf shape of *S. Gillii* subsp. *erysimoides* recall *Dubyaea* Sect. IXERIDOPSIS while the two sections also resemble each other in their relatively short corolla tubes. There are, therefore, one definite and two suggestive connections between *Dubyaea* and *Soroseris*. The relationship between *Soroseris* and *Youngia* is less evident, and is shown chiefly by the resemblance in habit, corollas, and pappus between *S. umbrella* and *Youngia depressa*. The short, deltoid outer bracts of *Youngia*, however, contrast sharply with the elongate, linear ones of *Soroseris*, while the achenes of the two genera are quite different. *Prenanthes* resembles *Soroseris* in its narrow, few-flowered involucres and in the shape of its achenes, but the limit of reduction in floret number is mostly five in *Prenanthes* and four in *Soroseris*, while the shape of the outer involucral bracts is quite different in the two genera. Furthermore, the two genera differ widely from each other in habit, and no species is known which suggests any direct connection between them. For this reason the writer believes that the similarities between *Soroseris*, *Youngia*, and *Prenanthes* are due merely to their common relationship with *Dubyaea*.

The connection between *Soroseris* and *Crepis* is still more remote. The differences between *Dubyaea* and *Crepis* in stigmas and achenes has already been mentioned; *Soroseris* is even more different from *Crepis* in these respects than is *Dubyaea*. In the shape of its involucres, as well as in the character of its styles, stigmas, pappus setae, and achenes, *Soroseris* is nearer to *Prenanthes* than to *Crepis*. The habital resemblance between *Crepis nana* Richards. and *Soroseris* is, in the opinion of the writer, merely a case of parallel evolution, in response to a similar ecological habitat.

C. nana has the short outer bracts, small corollas, slender, pale stigmatic branches, weak pappus bristles, slender, terete achenes, and the reduced floral anatomy most characteristic of *Crepis;* in all of these respects it differs more widely from *Soroseris* than do such *Crepis* species as *C. sibirica* and *C. kashmirica*, which in their habit show no resemblance whatever to *Soroseris*.

DIAGNOSIS OF SECTIONS OF SOROSERIS

SECTION 1. **Dubyaeopsis** sect. nov.—Leaves large, lyrate-pinnatifid with the lateral lobes much reduced, or merely elliptic to orbicular; involucres large with 10–15 inner bracts and 15–25 florets; inner bracts not thickened at maturity.

SECTION 2. **Eusoroseris** sect. nov.—Leaves small, entire or pinnatifid; involucres narrow, with 4–5 inner bracts and florets; inner bracts spongy-thickened at maturity.

ARTIFICIAL KEY TO THE SPECIES OF SOROSERIS

A. Leaves large, the blade mostly 3–6 cm broad; involucres with 10–15 inner bracts and 15–25 florets; inner bracts not thickened at maturity ..... 1. *S. umbrella*

A. Leaves less than 2 cm broad; involucres with 4–5 inner bracts and 4–5 florets; the inner bracts spongy thickened at the base at maturity.

B. Cataphylls numerous on the lower part of the stem; leaf blades elliptic or spatulate; ligule of corollas mostly equalling or shorter than the tube.

C. At least some heads of the inflorescence with 5 inner bracts and 5 florets; all of the inner bracts essentially similar, and with scarious margins ..... 2. *S. glomerata*

C. All of the heads with 4 inner bracts and 4 florets; inner bracts in two dissimilar pairs, the outer (lower) pair lanceolate and without scarious margins, the inner (uppermost) broader, often ovate or elliptic, and with more or less distinct scarious margins.

D. Leaf margins entire or remotely denticulate; involucres 10–15 mm long; ligule of corollas gradually contracted at the base, shallowly and evenly 5-dentate at the apex; anthers 3.5–5 mm long, yellowish.

E. Leaves on slender petioles, these 0.5–1.5 mm in diameter at the apex; involucres 10–13 mm long; lower pair of inner involucral bracts 1.5–2.5 mm broad, acute at the apex; western Himalaya and western Turkestan ..... 3. *S. Deasyi*

E. Petioles of leaves 2–4 mm broad at the base of the blade; western China and adjacent Tibet.

F. Involucres 11–13 mm long; lower pair of inner involucral bracts 2.9–3.2 mm broad, obtuse or acute at the apex ..... 4. *S. rosularis*

F. Involucres 12–19 mm long; lower pair of inner involucral bracts 1.5–2.5 mm broad, acute at the apex ..... 5. *S. bellidifolia*

D. Leaf margins coarsely dentate; involucres 7–9 mm long; ligules of corollas abruptly contracted at the base, deeply and unevenly 5-dentate at the apex; anthers 2.5–3.5 mm long, blackish or greenish ..... 6. *S. pumila*

B. Cataphylls few or none; leaf blades lanceolate or oblanceolate; ligules distinctly exceeding the tube of the corolla; anthers blackish or greenish.

G. Involucres 11–16 mm long; upper (innermost) pair of involucral bracts 3.2–4.5 mm broad; corolla tube 5.5–10.5 mm long; pappus setae 10–16 mm long ..... 7. *S. Gillii*

G. Involucres 7–12 mm long; uppermost pair of inner bracts 2–3.5 mm broad; corolla tube 3–6 mm long; pappus setae 6.5–11 mm long ..... 8. *S. Hookeriana*

1. **Soroseris umbrella** (Franch.) comb. nov. (Fig. 9, *a–e*).—Stems 5–18 cm long, mostly subterranean and rhizomatous; cataphylls numerous, the lower ovate, the upper lanceolate or linear; leaves on petioles 3–12 cm long, these sparsely hirsute, the blade glabrous or closely tomentulose, orbicular or lyrate-pinnatifid with a few small lobes below the large terminal one, 2–8 cm long, 1.5–6 cm broad; inflorescence densely cymose, peduncles 1.5–8 cm long, thick, simple or branched, bearing 1–4 small leaves or lanceolate bracts; involucres 14–20 mm high; outer bracts 2–4, broadly linear, equalling or somewhat shorter than the inner; inner bracts 10–15, lanceolate, acute, sparsely hirsute or glabrous, not thickened at maturity, coalescent at the base; florets 15–25; corollas yellow, 12–20 mm long, the tube slightly shorter than the ligule; anthers 3–5.5 mm long; achenes 3–6 mm long, narrowly oblong, slightly contracted at the apex, prismatic in cross section, stramineous, fuscous or olive green, smooth or lightly striate; pappus setae white, 9–11 mm long, deciduous at maturity. (*Crepis umbrella* Franch., Jour. de Bot. 9: 255, 1905.)

Western China and eastern Tibet, in alpine situations. The following are typical: CHINA: Szechuan Prov., Mt. Konka, alt. 5140 m, *Rock 16822* (B); Yunnan Prov., Likiang Snow Range, *Forrest 3004* (B, K); *Rock 5303* (B), 9846, 9926 (K), 25320 (UC); Mekong-Yangtze divide, alt. 3640–3940 m, *Forrest 20373* (K); Mountains of Hung-Po, alt. 4550 m, *Rock 23402* (UC). TIBET: Pa La, alt. 3333 m, *Ward* in 1924 (K).

The last named specimen differs from the typical Chinese *S. umbrella* in its coarsely dentate leaves, shorter anthers, and somewhat smaller achenes. It may represent a distinct subspecies. Another specimen from Tibet (Chumbi, *King's collector 586*, B) is in general similar to *S. umbrella*, but has much smaller involucres (10–12 mm long) more acute inner bracts and black achenes 3 mm long. It may represent a distinct species, but the material available is not sufficient for description.

Soroseris umbrella is a most distinctive species, and forms a connecting link between the other species and *Dubyaea* and *Youngia*. Its habit and leaves recall those of *S. Deasyi* and *S. rosularis*, except for size, so that these two species are perhaps the nearest relatives of *S. umbrella*.

2. **Sorosis glomerata** (Decne.) comb. nov. (Fig. 9, *f–g*)—Stems always short, chiefly subterranean and rhizomatous, 3–6 cm long; cataphylls numerous, broadly lanceolate to ovate; leaves mostly spatulate or obovate, on broadly winged petioles, the blade 6–10 mm long, 4–7 mm broad, 3-nerved, glabrous or slightly hirsute; inflorescence flat, cymose; heads on peduncles 0.5–6 mm long; involucres 10–12 mm long; outer bracts 2, linear, hirsute, slightly shorter than the inner; inner bracts 4 or 5, all with scarious margins, 1.5–3 mm broad, obtuse or acute at the apex, hirsute throughout with whitish, crisped trichomes or glabrate toward the base; florets 5; corollas white or perhaps sometimes yellow; 12.5–15 mm long, the tube 7–9 mm, the ligule 5.5–6 mm long; anther tube 3–4 mm long, greenish; style black, the branches of the

Fig. 9. *a–e*, *Soroseris umbrella*, *a–c* from *Forrest 10952* (UC); *d–e*, from *Rock 25320* (UC): *a*, habit, ×½; *b*, involucre, ×2; *c*, corolla, ×4; *d*, achene, ×8; *e*, pappus seta, ×8. *f–g*, *Soroseris glomerata*, from *Champion 52* (DD): *f*, leaf, ×1; *g*, involucre, ×2.

stigma 2.8–3 mm long; achenes 5–6 mm long, grayish brown, somewhat attenuate at the base, slightly contracted at the apex; pappus setae 6.5–7.5 mm long, silvery gray, somewhat paler toward the base. (*Prenanthes glomerata* Decne. ex Jacquem., Voy. Ind. 99, t. 107, 1834; *Crepis glomerata* Benth. et Hook. f., Gen. Pl. 2(1): 515, 1873; Hook. f., Fl. Brit. India 2: 398, 1882, in part; *Crepis sorocephala* Hemsl., Jour. Linn. Soc. 30: 116, t. 4, figs. 1–4, 1894.)

Central Himalaya in Garwhal and Almora provinces and Tibet, in stony or rocky situations at altitudes of 3800–5400 m. Only the following have been seen:

INDIA: Sumna, Almora Prov., alt. 4436 m, *Champion 52* (DD). TIBET: Chaldu, north of Antadhura Pass (Almora Province) alt. 4700 m, *Champion 51* (DD).

The plants of these two collections agree well with the description and illustration of *Prenanthes glomerata* Decne. (loc. cit.), as well as those of *Crepis sorocephala*. Hemsley (loc. cit.) listed three differences between his *C. sorocephala* and *S. glomerata:* "foliis carnosis, floribus albis, achaeniis oblongo-obovoideis." The original description of *P. glomerata* Decne. (loc. cit.) also characterizes its leaves as "carnosa" and the achene as "inferne subattenuatus," but makes no mention of the color of the flowers. The corollas on the specimens seen by the writer, which were collected in the same general region as Jacquemont's type, are pale, and were very likely white or cream color when fresh. Hence none of the differences listed by Hemsley may be said to hold.

True *Soroseris glomerata* has been very rarely collected, but may have a very wide range in Tibet. The two localities cited by Decaisne (loc. cit.) are "supra Ghauti" and "Kioubrang Ghauti." The former could not be accurately located on Jacquemont's map, but the latter is a pass east of the Sutlej River, and just north of the sources of the Ganges and Jumna Rivers (cf. Jacquemont, Voy, Ind., atlas). This would place it about on the border between what is now the province of Tehri Garwhal and Tibet. The two localities of Champion listed above are about 240 km east of this, while the type locality of *Crepis sorocephala* Hemsl. (Jour. Linn. Soc. 30: p. 102) is probably "west and north of Lhassa," about 1100 km east of the type locality of *S. glomerata*. The intervening region is almost or completely unknown botanically. No specimens of true *S. glomerata* have been seen from elsewhere in the Himalaya. Those from Kashmir are all *S. Deasyi* (v. infra), while the only species known from Sikkim are *S. Hookeriana* and *S. pumila*. The citation of the locality of *C. glomerata* by Franchet (Jour. de Bot. 9: 256) as "Kaschmir (Jacquemon)" is erroneous, as is evident from the previous discussion.

3. **Soroseris Deasyi** (S. Moore) comb. nov. (Fig. 10, *e–f*)—Stems short, 3–13, mostly 5–6 cm long, chiefly subterranean and rhizomatous; cataphylls numerous, lanceolate or linear, or the lowermost ovate; leaves on elongate, slender petioles, these mostly 0.5–1.5 mm in diameter at the apex (*in sicc.*), blades elliptic, obovate, or spatulate, 1–1.8 cm long, 0.5–1.5 cm broad, more or less definitely 3-nerved, their margins entire or denticulate, their apex rounded; inflorescence flat, cymose, the heads on peduncles 1–20 mm, mostly 5–6 mm long; involucres 10–13 mm long; outer bracts 2, linear, shorter than or exceeding the inner; inner bracts 4, hirsute, the lower (outer) pair 1.5–2.5 mm broad, acute at the apex, without scarious margins; the upper (inner) pair 2.5–4 mm broad, acute or obtuse at the apex, with broad scarious margins; florets 4; corollas yellow, the ligules blackish at the base, length of corolla 13–17 mm, the tube 7–9 mm, the ligule 6–8 mm long; anther tube 3.5–4.5 mm long, dark yellow or somewhat reddish (*in sicc.*); style greenish or blackish, the stigmatic branches 2–2.8 mm long; achenes yellowish or reddish, 5–6 mm long, somewhat attenuate at the base and slightly contracted at the apex; pappus setae dirty white to pale rufous, 9–11 mm long. (*Crepis glomerata* Hook. f., Fl. Brit. Ind. 3: 398, 1882, in part, not *Prenanthes glomerata* Decne.; *Lactuca Deasyi* S. Moore, Journ. Bot. 38: 428, 1900.)

Western Himalaya in Kashmir and Punjab, north to Chinese Turkestan (Sinkiang). Rocky talus slopes and gravel slides at 4000–5000 m. The following have been seen (all but the last identified as *Crepis glomerata*):

INDIA: Kashmir Prov., Har Nag, Upper Lidar Valley, alt. 4212 m, *Stewart 12389* (UC, K, B, G, NY); Mt. Kolahai, alt. 4212 m, *Stewart 9420* (K); Dessai Baltistan, alt. 4212 m, *Meebold 980* (B); Pir Panjal, *Duthie 25659* (K); Lahul, *Edgeworth 5040* (K); Zoypal, alt. 4090 m, *Coventry 928* (K); Punjab Prov., without locality, *Drummond 25561* (K). CHINESE TURKESTAN (Sinkiang): Aksu, alt. 5000 m, *Deasy 95* (type of *Lactuca Deasyi* S. Moore, in herb. British Museum, photo and fragments UC).

S. Deasyi is the species of Kashmir which has generally passed as *Crepis glomerata*. A photograph and fragments of the type specimen of *Lactuca Deasyi* show beyond any doubt that it belongs in the same genus with *Soroseris glomerata*. It matches fairly well a considerable series of specimens from Kashmir, which differ from true *S. glomerata* in their larger leaves, larger heads, involucres with four inner bracts, the lower pair of which have no scarious margins, in the length and color of the pappus setae and other details. In fact, the affinity of *S. Deasyi* is much closer to *S. rosularis* of Yunnan and *S. bellidifolia* of northwestern China than to *S. glomerata*.

4. **Soroseris rosularis** (Diels) comb. nov. (Fig. 10, *a–d*)—Stems short, 2–10 cm long, chiefly subterranean and rhizomatous; cataphylls numerous, ovate or lanceolate; leaves on broad, elongate petioles, 1.5–7 cm long, 2–4

mm broad at the base of the blade; blades spatulate, obovate, or elliptic, 1–2 cm long, 0.5 cm broad, obtuse or rounded at the apex, inconspicuously 3-nerved, the margins entire or remotely denticulate; the margins and upper part of the petiole hirsute, becoming glabrate in age; inflorescence flat, cymose, peduncles 2–6 mm long; involucres 11–13 mm long; inner bracts 4, lightly hirsute, the lower pair obtuse or acute at the apex, 2.8–3.2 mm broad, without scarious margins, the upper pair rounded at the apex, 4.5–5.5 mm broad when fully spread out; florets 4; corollas yellow, the base of the ligule and upper part of the tube black, 12.5–15.5 mm long, the tube 6–8.5, the ligule 6–7 mm long; anthers yellowish, 3.5–4 mm long; style blackish, the stigmatic branches 2–2.8 mm long; achenes not seen; pappus setae 8.5–10.5 mm long, stramineous or pale rufescent. (*Crepis rosularis* Diels, Notes Roy. Bot. Gard. Edinb. 25: 201, 1912.)

Yunnan Province, China, in limestone rocks at 3300–4000 m. The following have been seen:

CHINA: Yunnan, eastern flank of Lichiang Range, Lat. 27° 30′ N, alt. 3333–3636 m, *Forrest 6093* (UC, K, B), *10461* (UC, B); same locality, *Rock 4479, 5474* (B); same locality, *Schneider 2065* (B).

This species is so close to *S. Deasyi* that, were it not for the great separation in the range of the two, they might be considered subspecies of the same species. *S. rosularis*, however, has consistently broader petioles and involucral bracts than *S. Deasyi*, while the leaves are less conspicuously 3-nerved. As described by Franchet (Jour. de Bot. 9: 256, 1895), the lateral nerves of the leaves of *S. glomerata* and *S. Deasyi* diverge from the median one at or near the base of the blade, while in *S. rosularis* the laterals run parallel to the median nerve for $\frac{1}{3}$ to $\frac{1}{2}$ of the distance from base to apex of the blade, so that the blade appears 1-nerved, at least in its lower half. There is, however, considerable variation in this characteristic, even among the different leaves on the same plant, and the distinction between *S. Deasyi* and *S. rosularis* in this respect is not sharp. As described by Franchet (loc. cit.), this apparently one-nerved condition of the leaves is more pronounced in *S. Hookeriana* and *S. Gillii* (="*C. trichocarpa*").

5. **Soroseris bellidifolia** (Hand.-Mazz.) comb. nov. (Fig. 10, *g–i*)—In habit like the last two, but more robust; stems 8–11 mm long; cataphylls numerous, ovate or lanceolate; leaves on petioles 5–8 cm long and 2–4 mm broad; the blade obovate or elliptic, 1.5–2.5 cm long, 0.8–1.5 cm broad, its apex obtuse or rounded, its margin entire or remotely denticulate; inflorescence flat, cymose; involucres 12–15 mm long; outer bracts 13–20 mm long; inner bracts 4, conspicuously hirsute, the lower pair acute, 1.5–2.5 mm broad, the upper pair acute or obtuse, 4.5–5.5 mm broad, narrowly elliptic in outline, tapering conspicuously toward the apex; florets 4; corollas 20 mm long, yellow, the base of the ligule and apex of the tube black, the tube 10 mm, the

ligule 10 mm long; anthers yellowish (or blackish?), 5 mm long; achenes reddish brown, tapering toward the base and slightly contracted at the apex, 8 mm long; pappus setae deep yellow or somewhat rufous at the base, grayish at the apex, 10–11 mm long. (*Crepis Gillii* var. *bellidifolia* Hand. Mazz., Acta Horto Goth. 12: 355, 1938.)

Western China, from Kansu to Yunnan Provinces. The following is the only typical specimen seen:

China: Southwestern Kansu Prov., Minshan, west of Shimen range, 4100 m, *Rock 13025* (UC, B, K).

The writer has not been able to see the type of *Crepis Gillii* var. *bellidifolia*, so that the present description is based on the Rock collection also cited by Handel-Mazzetti, and from the same general region.The specimens of this collection are obviously more closely related to S. *rosularis* and *S. Deasyi* than to *S. Hookeriana* and *S. Gillii*. They have the numerous cataphylls characteristic of the two former (although these are not clearly visible on any except the UC specimen, which is the only one that is mounted with the outside of the stem up), and agree with them in leaf shape and in the long corolla tube.

S. bellidifolia resembles *S. rosularis* in its broad petioles and *S. Deasyi* in its narrow, more or less acute involucral bracts, but differs from both of these species in its more robust habit, somewhat longer involucres, larger corollas, larger achenes, and in the color of its pappus. One collection from Yunnan, on the Mekong-Yangtze divide, east of Yeh-chih, alt. 3940–4240 m, *Forrest 20367* (part, UC, B), contains specimens which agree with *S. bellidifolia* in their general appearance and the color of the pappus, but which in the shape of the involucral bracts, the relative length of the corolla tube and ligule, and to some extent the leaf shape, are transitional toward *S. Hookeriana* subsp. *erysimoides* and *S. Gillii* subsp. *hirsuta*. Since a specimen of the latter subspecies is on the Berlin sheet of the same collection, the transitional forms may be the result of hybridization between *S. bellidifolia* and *S. Gillii*. Their pollen is somewhat more irregular than that of *S. rosularis*, and contains about 20% of obviously defective grains. No pollen of *S. bellidifolia* was available. If many more localities are found in which transitional forms like this occur, the different species here recognized may have to be combined, but the wisest course at present is to keep them separate, even though they are not sharply differentiated from each other.

6. **Soroseris pumila** sp. nov. (Fig. 10, *j–q*)—Radix tenuis, ad apicem 3–7 mm crassa; caulis rhizomatus, tenuis, 2.5–10 cm longus, ad mediam 2–8 mm crassus, ad apicem in inflorescentiam expansus, cataphyllis pluribus obsita,

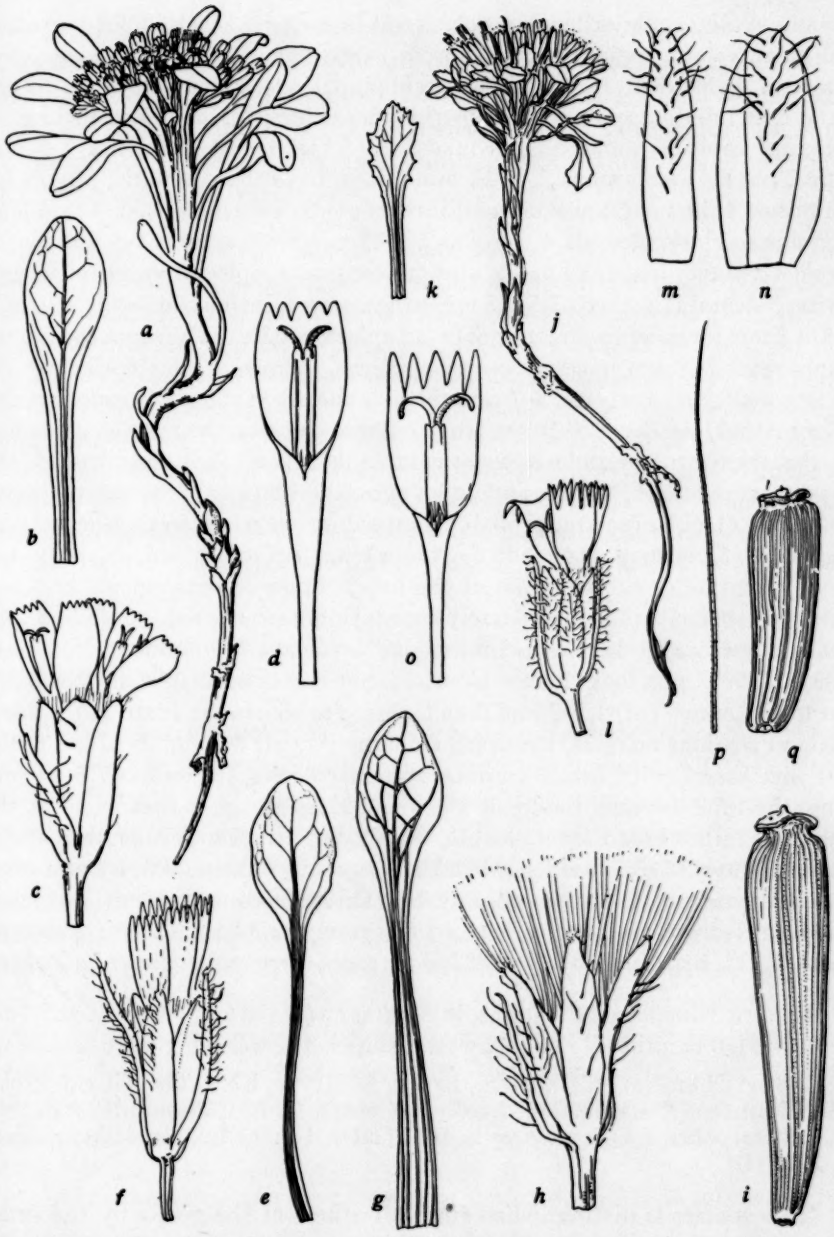

Fig. 10. *a–d*, *Soroseris rosularis*, from *Forrest 1046* (UC): *a*, habit, ×½; *b*, leaf ×1; *c*, involucre, ×2; *d*, corolla, ×4. *e–f*, *Soroseris Deasyi*, from *Stewart 12389* (UC). *e*, leaf, ×1; *f*, involucre, ×2. *g–i*, *Soroseris bellidifolia*, from *Rock 13025* (UC): *g*, leaf, ×1; *h*, involucre, ×2; *i*, achene, ×8. *j–q*, *Soroseris pumila: j–o*, from type, *p–q*, from *Hooker* s.n.; *j*, habit, ×½; *k*, leaf, ×1; *l*, involucre, ×2; *m*, *n*, inner bracts, ×4; *o*, corolla, ×4; *p*, pappus seta, ×8; *q*, achene, ×8.

infimis ovatis, superioribus lanceolatis vel linearibus, acutis; folia spatulata vel oblanceolata, petiolis tenuis 1–5 cm longis, lamina 5–20 mm longa, 3–9 mm lata, valde dentata vel ad basim subpinnatifida, apice obtusa vel rotundata, folia inferiora sparse, folia superiora dense hirsuta; inflorescentia discum formans, capitulis numerosis, pedunculis 2–5 mm longis; involcura 7–9 mm longa, phyllis exterioribus 2, 9–12 mm longis, linearibus, hirsutis, phyllis interioribus 4, hirsutis, apice obtusis, intimis ovatis vel ellipticis, 3–4 mm latis margine scariosis; floscula 4; corollae 7.5–11 mm longae, tubo 3–5 mm longo, ligule 4.5–6 mm longa, ad basim abrupte contracta, apice profunde et irregulariter 5-dentata; antheris 2.5–3.5 mm longis, nigrescentibus (in sicc.); achaenia 3.5–4.2 mm longa ad basim attenuata, ad apicem paullo sed abrupte contracta; pappi setae 7–8 mm longae argenteae, griseae, vel rarius lutescentiae.

Root slender, elongate, 3–7 mm thick at the apex; stem subterranean and rhizomatous, slender, 2.5–10 cm long, 2–8 mm thick at the middle, expanded at the apex into the inflorescence; cataphylls several and conspicuous, the lowermost ovate, the middle and upper ones lanceolate or linear, acute; leaves spatulate or oblanceolate, probably purplish-green when fresh, the petioles slender, 1–5 cm long, the blade 5–20 mm long, 3–9 mm broad, coarsely and closely dentate or subpinnatifid at the base, obtuse or rounded at the apex, the lower sparsely, the upper densely hirsute; inflorescence flat, corymbose, the heads numerous, peduncles 2–5 mm long; involucres 7–9 mm long, the outer bracts 2, 9–12 mm long, linear, hirsute, inner bracts 4, hirsute, in two pairs, the lower (outer) pair 1.5–2 mm broad, obtuse or somewhat acute at the apex, without scarious margins, the upper (innermost) pair 3–4 mm broad, elliptic, 3–4 mm broad, with broad scarious margins; florets 4; corollas 7.5–11 mm long, the tube 3–5 mm, the ligule 4.5–6 mm long, abruptly contracted at the base and rather broad for its length, deeply and irregularly 5-dentate at the apex; anthers 2.5–3.5 mm long, blackish (*in sicc.*); achenes 3.5–4.2 mm long, attenuate toward the base, slightly but abruptly contracted at the apex; pappus setae 7–8 mm long, silvery gray or rarely yellowish. (*Crepis glomerata* Hook. f., Fl. Brit. India 3: 398, 1882 in part, not *Prenanthes glomerata* Decne.)

Eastern Himalaya Mountains, in Sikkim and adjacent Tibet, at altitudes of 3940–5150 m, probably on rocky talus slopes. The following have been seen:

TIBET: Chumolari, alt. 4850 m, *Lepcha 527* (type, K). INDIA: Sikkim Prov., Kinchin jharo (?) alt. 4850 m, *Hooker* s.n. (part, K. B); Sikkim, *Elwes* in 1877 (K); Mizarpohri, *King's collector* in 1887 (DD); Guiche La, alt. 4390 m, *Ghose* in 1932 (UC).

This species is distinguished from all others of the genus by the small size, both of its vegetative and floral parts, as well as by the shape and peculiar dentation of its leaves. Furthermore the ligules of the corollas are remarkably broad for their length and, in the specimens examined, are more deeply and irregularly toothed at the apex than are those of any other species of *Soroseris*. On the basis of its habit, its numerous cataphylls, the

shape of its leaves, and the relative length of corolla tube and ligule, *S. pumila* is closest to *S. Deasyi* and *S. rosularis*, from both of which it differs in its blackish anther tubes, as well as in the characters mentioned above. Phylogenetically it may be considered the most reduced and specialized species of the genus, and is probably an offshoot from the complex of *S. Deasyi* and *S. rosularis*.

7. **Soroseris Gillii** (S. Moore) comb. nov. (Fig. 11, *a–h*)—Stems mostly short, 2–12 cm tall; cataphylls few or none; leaves lanceolate, pinnatifid or dentate; inflorescence flat, cymose, often very broad; involucres 11–16 mm long, inner bracts 4, glabrous or hirsute, acute or obtuse at the apex, the lower pair 1.6–2.5 mm broad, without scarious margins, the upper pair 3.2–4.5 mm broad, with scarious margins; florets 4; corollas yellow, the base of the ligule and apex of the tube blackish, 14.5–21.5 mm long, the ligule equalling or somewhat longer than the tube; anthers blackish (*in sicc.*), 4–6 mm long; branches of the stigma 2–3 mm long; achenes 3–6 mm long, blackish when mature, obovoid, the lower pair definitely obcompressed, the upper pair subterete; pappus setae rufous, stramineous, or grayish at the summit, 10–16 mm long.

Western China to the Western Himalaya, in meadows, gravelly places and talus slopes (screes) at 3700–5000 m altitude.

The distinction between *S. Gillii* and *S. Hookeriana* is chiefly in the size of the floral parts, *S. Gillii* being larger throughout. There is little or no overlapping in at least some characteristics, such as the length of the corolla tube and the breadth of the innermost involucral bracts, while there is an accompanying difference in habit, since *S. Hookeriana* generally has well developed stems, while *S. Gillii* rarely has. Furthermore, both *S. Gillii* subsp. *typica* and *S. Hookeriana* subsp. *erysimoides* have been collected in the vicinity of Tatsienlu, western Szechuan, but the specimens show no sign of intergradation between the two. Further collections, particularly from the critical region of southwestern Szechuan and northwestern Yunnan, may make necessary the uniting of *S. Gillii* under *S. Hookeriana*, but at present the writer feels justified in maintaining them as separate species.

Four subspecies may be recognized under *S. Gillii*, as follows:

A. Inner involucral bracts mostly obtuse or rounded at the apex, dark green or blackish in color, glabrous, short pubescent, or sparsely hirsute; pappus rufous or stramineous.

B. Involucres 13–16 mm long; the inner bracts glabrous or short-pubescent; anthers 5–6 mm long; pappus setae 12–15 mm long.....a. subsp. *typica*

B. Involucres 11–12 mm long, the inner bracts sparsely hirsute along the midrib; anthers 4 mm long; pappus setae 10–10.5 mm long.....b. subsp. *Handelii*

A. Inner involucral bracts mostly acute at the apex, greenish or yellowish, sparsely to strongly hirsute; pappus setae grayish at least at the apex.
  C. Leaves runcinate-pinnatifid; inner bracts densely hirsute; pappus setae 12–14 mm long; Yunnan and adjacent Tibet.....c. subsp. *hirsuta*
  C. Leaves sinuate-pinnatifid, sinuate-dentate, or merely denticulate; inner bracts sparsely to moderately hirsute; pappus setae 10–15 mm long; western Himalaya.....d. subsp. *occidentalis*

7-a. **Soroseris Gillii typica** nom. nov. (Fig. 11, *a–b*)—Leaves runcinate-pinnatifid, the blade 3–8 cm long, 0.7–1.8 cm broad; inflorescence flat, cymose, the heads very numerous, on peduncles 2–12 mm long; involucres 13–17 mm long, the inner bracts glabrous or rarely short-pubescent, dark green or blackish at least toward the apex, the apex obtuse or rounded; corolla tube 8–10.5 mm long, the ligule 9–12 mm long; anthers 5–6 mm long; achenes 3–6 mm long; pappus setae 13–16 mm long, rufous. Chromosome number, 2n = 16. (*Crepis trichocarpa* Franch., Jour. de Bot. 9: 257, 1895 (?); *Crepis Gillii* S. Moore, Jour. Bot. 47 (1899): 170; Hand.-Mazz. Acta Horto. Goth. 12: 355, 1938, pro parte, vars. *erysimoides* et *bellidifolia* exclusae).

Western China and adjacent Tibet. The following have been seen:

China: Szechuan Prov.; near Tachienlu, *Pratt 456, 482, 875* (K); Tatsienlu, *Soulié 2160* (B); Tongolo, *Soulié 2663, 2664* (B); Baurong to Tachienlu via Hadjaha, *Stevens 178, 379* (B); Mt. Mitzuga, west of Muli Gomba, alt. 3050–4875 m, *Rock 16242* (B); north of Chiu-Lung-Hsien, Minya Country, alt. 5000 m, *Rock 17449* (B); between Litang and Yalung Rivers, alt. 4400 m, *Rock 16630* (B); between Litang and Shou-Chu Rivers, alt. 4510 m, *Rock 16756* (B); Kaushu shan, Leirong, alt. 4090 m, *Rock 24094, 24502* (UC). Tibet: between Labrang and Yellow River, alt. 3700 m, *Rock 14529* (UC, B, K). The last specimen transitional toward subsp. *occidentalis*.

Handel-Mazetti (loc. cit.) rejected Franchet's *Crepis trichocarpa* on the grounds that the type specimen did not possess pubescent achenes as described and emphasized by Franchet. The writer has not seen this type, but since pubescent achenes have not been seen on any species of this genus, the opinion of Handel-Mazzetti, that Franchet's description is based on a *planta composita*, is probably correct.

7-b. **Soroseris Gillii Handelii** subsp. nov. (Fig. 11, *c–d*)—A subsp. typica differt involucris 11–12 mm longis, phyllis interioribus ad apicem sparse hirsutis; corollis 15–16 mm longis, tubo 7–8 mm, ligula 8.5–9 mm longa; antheris 4 mm longis; pappi setis 10–10.5 mm longis.

Leaves runcinate-pinnatifid or sinuate-dentate, the blade 2–4 cm long, 0.5–1.3 cm broad; involucres 11–12 mm long, the inner bracts dark green or blackish, sparsely hirsute toward the apex, the apex obtuse or rounded; corolla tube 7–8 mm, the ligule 8.5–9 mm long; anthers 4 mm long; pappus setae stramineous or rufous, 10–10.5 mm long.

Southwestern China. The following have been seen:

China: southwestern Szechuan, Döko range, above Muli monastery, alt. 4350 m, *Handel-Mazzetti 7417* (type, B); Yunnan, Che-tse-lo, top of Pi-lo-shan. alt. 4000 m, *Tsai 58037, 58192* (UC, G).

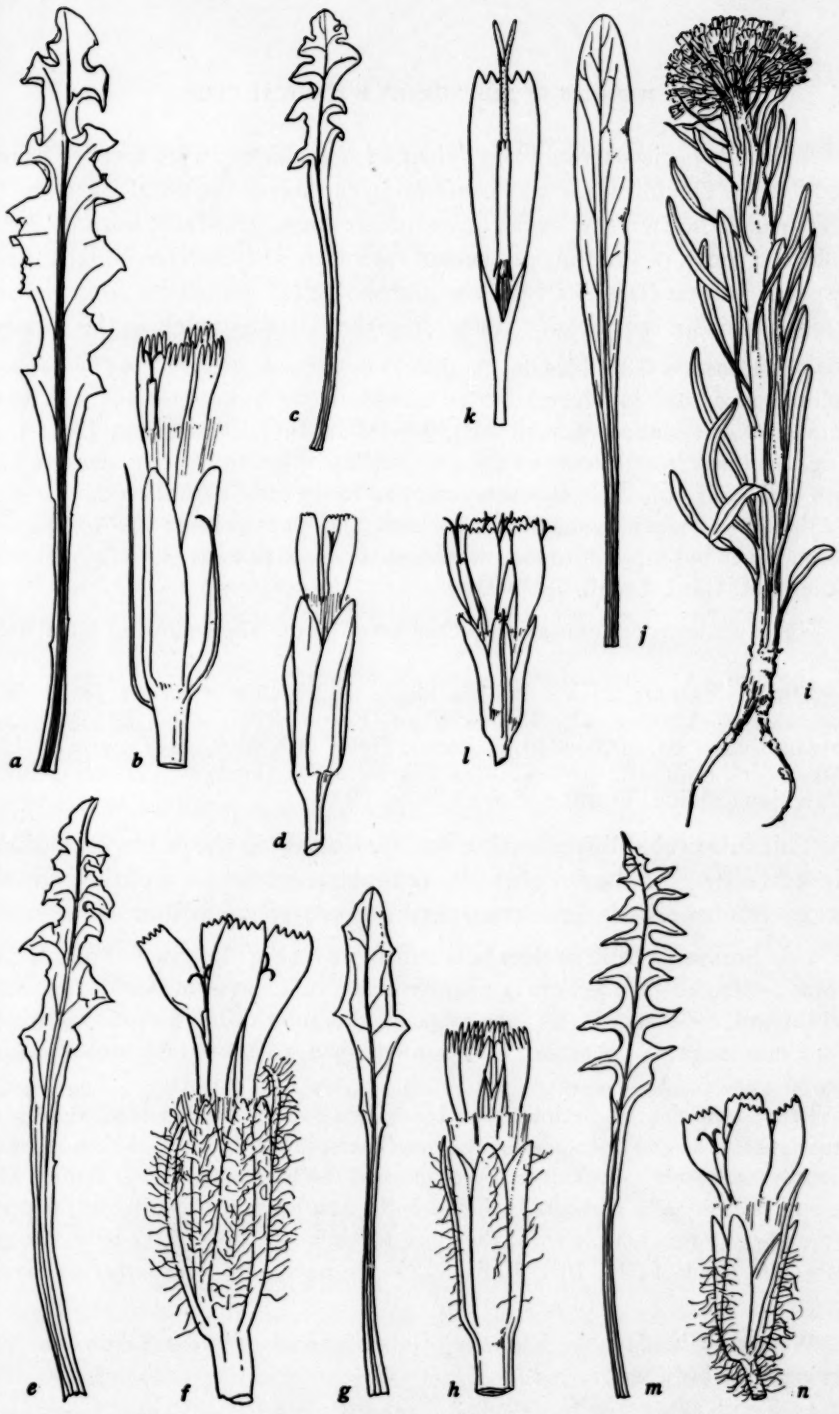

Fig. 11. *a–h*, *Soroseris Gillii*: *a–b*, subsp. *typica*, from *Rock 16630* (UC): *a*, leaf, ×1; *b*, involucre, ×2; *c–d*, subsp. *Handelii*, from type (B); *c*, leaf, ×1; *d*, involucre, ×2; *e*, *f*, subsp. *hirsuta*, from *Forrest 19054* (B): *e*, leaf ×1; *f*, involucre, ×2; *g*, *h*, subsp. *occidentalis*, from type (K): *g*, leaf, ×1; *h*, involucre, ×2. *i–n*, *Soroseris Hookeriana*: *i–l*, subsp. *erysimoides*, from *Rock 12645* (UC, G): *i*, habit, ×½; *j*, leaf, ×1; *k*, involucre, ×2; *l*, corolla, ×4; *m–n*, subsp. *typica*, from *Hooker*, s.n. (K).

This subspecies differs from subsp. *typica* chiefly in its smaller heads and florets. The former is very constant in the size of the floral parts, however, while the two specimens cited under subsp. *Handelii*, both of them collected south of the range of subsp. *typica* are also closely similar in this respect. Subsp. *Handelii* forms a morphological transition from subsp. *typica* to subsp. *occidentalis*, resembling the latter as much as the former.

7-c. **Soroseris Gillii hirsuta** (Anthony) comb. nov. (Fig. 11, *e–f*)—Leaves, inflorescence, and involucral bracts conspicuously hirsute; leaves runcinate pinnatifid, the blade 2–4.5 cm long, 0.5–1.3 cm broad; involucres 12–15 mm long, the inner bracts acute at the apex, yellowish-green in color, densely hirsute with long, whitish trichomes; corollas 15–19 mm long, the tube 5.5–6.5, the ligule 9–12 mm long; anthers 4.8–5 mm long; pappus setae 12–14 mm long, stramineous but grayish toward the apex. (*Crepis Gillii* var. *hirsuta* Anthony, Notes Bot. Gard. Edinb. 18: 193. 1934.)

Northwestern Yunnan and southeastern Tibet. The following have been seen:

CHINA: Yunnan Prov., Bei-ma Shan, alt. 4240 m, *Forrest 14500* (B); northeast of Atuntze, alt. 4240–4540 m, *Forrest 20059* (UC, B); Mekong-Salwin divide, alt. 4090–4240 m, *Forrest 20088* (B); Mekong-Yangtze divide, east of Yeh-chih, alt. 4090–4240 m, *Forrest 20367* (part, B). TIBET: Salwin-Kiu-chiang divide, Tsarong, *Forrest 19054* (B).

This subspecies differs from subsp. *typica* only in the pubescence of the plant, the shape and color of the inner bracts, and the color of the pappus, but each subspecies is quite constant in these respects within its range.

7-d. **Soroseris Gillii occidentalis** subsp. nov. (Fig. 11, *g–h*)—Folia lanceolata, 2–4 cm longa, 0.5–1 cm lata, apice acuta, runcinato-pinnatifida, dentata, vel integra; involucra 11–14 mm longa, phyllis interioribus hirsutis; achaenia 5–6.5 mm longa; pappi setae 11–12.5 mm longae, ad apicem griseae, ad basim stramineae.

Leaves on slender petioles, the blade lanceolate, 2–4 cm long, 0.5–1 cm broad, acute at the apex, shallowly runcinate-pinnatifid, coarsely dentate, or sometimes merely denticulate; involucres 11–14 mm long, rather lightly hirsute or occasionally glabrate; achenes 5–8.5 mm long, reddish brown; pappus setae 11–12.5 mm long, gray at the apex, stramineous toward the base. (*Crepis glomerata* Hook. f., Fl. Brit. India 3: 398, in part, not *Prenanthes glomerata* Decne.)

Western Himalaya in Kumaon, Garwhal, and adjacent Tibet. The following have been seen:

INDIA: Garwhal Province (Tehri) Gangotri, alt. 4240–4550 m, *Keshavanand 31* (K, *type;* DD); Dudu Gadh, alt. 4550–4700 m, *Duthie 824* (K,DD); Kalajowar, *Strachey and Winterbottom 2* (G); Kumaon Province, Ralam Valley, *Duthie 24526* (K, DD); Barji Kang, *Strachey and Winterbottom 2* (K). TIBET: Meyin Madden, *Strachey and Winterbottom 2* (K).

This subspecies is very close to subsp. *hirsuta*, a surprising fact considering the distance that separates them. The exact relationships between these two subspecies, as well as between subsp. *occidentalis* and *C. Hookeriana* subsp. *typica*, will be clearer when more is known about the *Soroseris* flora of Nepal and southeastern Tibet.

8. **Soroseris Hookeriana** (C. B. Clarke) comb. nov. (Fig. 11, *i–n*)—Stems sometimes short, but more often well developed, 4–35 cm tall; cataphylls few or none; leaves lanceolate or oblanceolate, runcinate-pinnatifid, dentate, denticulate, or entire; inflorescence flat, hemispherical or ovoid; involucres 7–12 mm long; inner bracts 4, olive or blackish green, sometimes paler below, glabrous, hirsute toward the base, or rarely hirsute throughout, the lower pair 1.2–2 mm broad, usually acute at the apex, the upper pair 2–3.5 mm broad, with broad, scarious margins, acute, obtuse, or sometimes rounded at the apex; florets 4; corollas 10–17 mm long, the tube 3–6 mm, the ligule 6.5–12 mm long; anthers blackish or greenish, 3.5–5.5 mm long; mature achenes columnar, obovoid, or occasionally fusiform, all nearly terete, 3.5–6.5 mm long; pappus setae gray or stramineous toward the base, 6.5–11 mm long.

Eastern Himalaya north to northwestern China, in meadows, stony pastures, and talus slopes (screes), at altitudes of 3300–5100 m.

This is the most widespread and the most frequently collected species of *Soroseris*. It is the only one in which well developed, hollow stems are usually found. Its range is in general similar to that of *S. Gillii*, but in Western China *S. Gillii* is confined to the southern part (Yunnan, southwestern Szechuan), while *S. Hookeriana* occurs principally farther north (Kansu, Shansi) and extends southward through Tibet to the Sikkim Himalaya. Two subspecies of *S. Hookeriana* may be recognized and distinguished by the following key:

Leaves pinnatifid, acute at the apex; upper leaves, bracts of the inflorescence and peduncles strongly hirsute; pappus setae 7–9 mm long ..... a. subsp. *typica*

Leaves entire or denticulate, obtuse at the apex; upper leaves, bracts of the inflorescence and peduncles glabrous or sparingly hirsute ..... b. subsp. *erysimoides*

8-a. **Soroseris Hookeriana typica** nom. nov. (Fig. 11, *m–n*)—Stems 4–20 cm tall, hollow; leaves lanceolate, the blade 2–7 cm long, 0.3–1.5 cm broad, pinnatifid, the lobes and apex acute; upper leaves, bracts of the inflorescence, peduncles, and outer involucral bracts densely hirsute with long, yellowish trichomes; involucres 8.5–10 mm long; inner bracts glabrous, hirsute at the base, or occasionally hirsute throughout; pappus setae 7–9 mm long, grayish at the summit, dirty white, stramineous or yellowish on the lower part. (*Crepis Hookeriana* C. B. Clarke, Comp. Ind. 255, 1876, non Bal.; *Crepis glomerata* Hook. f., Fl. Brit. India 3: 398, 188, in part, not *Prenanthes glomerata* Decne.).

Eastern Himalaya, in Sikkim and adjacent Tibet. The following have been seen:

INDIA: Sikkim Prov., 4240–4850 m, Ghora la (?), Karkole (?), Hooker s.n. (in part) (K, B, G, NY); Tankra Mt., alt. 4090 m, *Gammie 421* (K); Ghora La, alt. 4850 m, *Bibu and Rhomoo 5173* (K); Boktu, alt. 4090 m, *Ghose* in 1932 (UC); Tango (?), alt. 4240 m, *Smith and Cave 2500* (B); Le lap la, *King* in 1877 (DD); Lugnak la, *Wager 269* (K). TIBET: Yatung, *Hobson* in 1897 (K); Chumolari, alt. 4850 m, *Lepcha 519* (K); Lonok, *Younghusband 217* (B); Tang la, eastern Himalaya, *Ward 5946* (K). The last specimen is transitional toward subsp. *erysimoides*.

The specific name *Hookeriana*, though invalid in *Crepis* for this species, can be used in *Soroseris*, since no other specific name exists for the species as here recognized. The case is quite parallel to that of *Dubyaea atropurpurea* (Stebbins Jour. Bot. 1937:51).

The collections of Hooker from Sikkim, all of them identified by him as *Crepis glomerata*, include three different forms. That described above is represented by one full sheet in the Kew Herbarium, which is probably the type sheet of Clarke's *C. Hookeriana*. It agrees very well with the description of Clarke (loc. cit.). Three plants of subsp. *typica* are on the sheet in the Berlin Herbarium, two on that in the Gray Herbarium, and one in the New York Botanical Garden sheet. The second sheet in the Kew Herbarium contains mostly plants of *S. pumila*, but in addition two of *C. Hookeriana* subsp. *erysimoides*. The latter subspecies also appears (though not always in its typical form) on all of the other sheets. The three forms were evidently collected in different localities, judging from the rough labels on the Kew sheets. The writing on these labels is almost illegible to the present author, but the best possible interpretations of these localities are given with the citations.

8-b. **Soroseris Hookeriana erysimoides** (Hand.-Mazz.) comb. nov. (Fig. 11, *i–l*)—Plants mostly glabrous throughout; stems 4–25 cm tall, hollow; leaves numerous, oblanceolate, lanceolate, or linear, the blade 2–7 cm long, 1.5–11 mm broad, its margin entire, undulate, or minutely and remotely denticulate, its apex obtuse or rounded; involucres 7–12 mm long, the inner bracts glabrous or sparingly hirsute; pappus setae 7–9 mm (rarely 11 mm) long, grayish, or whitish below, rarely stramineous. (*Crepis Gillii* var. *erysimoides* Hand.-Mazz., Acta Horto Goth. XII: 355. 1938.)

Eastern Himalaya, where it passes into subsp. *typica*, north through eastern Tibet to western and northwestern China. The following have been seen:

INDIA: Sikkim Prov., Zemutory (?), alt. 3940–5150 m, *Hooker*, s.n. (in part, K, G, NY, B). BHUTAN: Do-tha, *Dungboo 265* (K). TIBET: Sham Man (?) Chumbi and Phari, *Dungboo* in 1879 (B); Chumighata, eastern Himalaya, alt. 4850 m, *Lepcha 77* (K); Dzomo La, between Radja and Jupar Range, alt. 4060 m, *Rock 14386* (UC, B); Wanchen nira, between Labrang and Yellow

River, alt. 4060 m, *Rock 14517* (UC, B); Amnyi Machen Range, *Rock 14442* (UC, B). CHINA: Shensi Prov., Tai pa shan, *Leason* in 1910 (K); *Giraldi 309, 3049, 3052* (B); Miao-wang-shan, *Giraldi 3051* (B); Tsin Ling Shan, alt. 3350 m, *Limpricht 2747* (B); Kansu Prov., Tangut region, *Przewalski* in 1872 (B); Sin hong shan and Ma ho shan, *Licent 4408* (K); west of Adjuan, alt. 3640 m, *Rock 12645* (UC, B); Szechuan Prov., Sungpan Hsien, *Fang 4027* (K, B, G); Ta Tsien Lu, *Soulie* 2159 (B); Tongolo, *Soulie 836* (K); Yunnan Prov., Bei Ma Shan, alt. 4240–4540 m, *Forrest 14516* (K, B), *20943* (UC, B); same locality, *Rock 9993* (B); Mekong-Salween divide, alt. 3940–4240 m, *Forrest 19712* (K). (The last specimen transitional toward *S. Gillii*.)

Subsp. *erysimoides* is the more distinctive and widespread of the two subspecies of *S. Hookeriana*. It is very constant throughout the center of its range. In the eastern Himalaya it appears to pass gradually into subsp. *typica*, which subspecies may be regarded as intermediate between subsp. *erysimoides* and *S. Gillii* subsp. *occidentalis*. As mentioned above, one of the main reasons for maintaining *S. Hookeriana* and *S. Gillii* as distinct species is the striking morphological discontinuity between *S. Gillii* subsp. *typica* and *S. Hookeriana* subsp. *erysimoides* in western China, where the ranges of the two overlap. If, however, further exploration of the eastern and central Himalaya shows that *C. Gillii* subsp. *occidentalis* intergrades with *C. Hookeriana* subsp. *typica*, the two species will have to be merged. Some of the specimens from Northern China (*Giraldi* nos. 3049, 3051, 3052) are transitional toward *C. Gillii* also. When more material is available from this region, these may be found to constitute a distinct subspecies, characterized by larger involucres, hirsute bracts, and stramineous pappus.

V. LACTUCA, SECTION AGGREGATAE

LACTUCA, Sect. AGGREGATAE Franch. Jour. de Bot. 9: 257, 1895. Plants with the habit of *Soroseris;* stems very short, expanded at the apex, the heads closely crowded and sessile or subsessile at its summit; involucres with 4–6 bracts, all of which are similar in length and in general outline; achenes slightly or strongly obcompressed, strongly contracted at the apex, 3–5 ribbed. Three species known, natives of Tibet and the mountains of western China.

The species of this section resemble superficially those of *Soroseris*, but there are definite differences between the two, even in habit. The larger leaves in Sect. AGGREGATAE have petioles which are sharply dilated into a sheathing base, while in *Soroseris* the petioles are uniform in breadth. The heads of these *Lactuca* species are sessile or on very short peduncles less than 2 mm long, while in *Soroseris* the peduncles are always well developed. Finally, the involucres of the species of *Soroseris* all have two or more narrowly linear or filiform outer bracts subtending the main series of broadly linear, lanceolate or elliptic inner ones, while in the Sect. AGGREGATAE these are altogether lacking.

In floral characteristics, the two groups are still more different. The corollas of these *Lactuca* species are purple or blue, colors not found in *Soroseris*, while the corolla tube is very long and slender, a characteristic feature of many *Lactuca* species, but not of *Soroseris*. The pollen grains have the echinolophate pattern characteristic of *Lactuca* and other Cichorieae but not of *Soroseris* (cf. Figure 8). The achenes are more abruptly contracted at the apex than are those of *Soroseris*, and have fewer ribs. *L. porphyrea* and *L. disciformis* have ovaries with 5 vascular bundles, a condition anomalous in *Lactuca*, but found in some other Asiatic species, such as *L. melanantha* Franch. and *L. chungkingensis* Stebbins (Stebbins 1937a). The supernumerary vascular bundles of the ovary so characteristic of *Soroseris* (p. 000) are, however, lacking, as in all other species of *Lactuca*. Finally, the pappus setae of Sect. AGGREGATAE are typical of *Lactuca* in being slender, fragile, and some are only 4-celled in cross section at the base (Fig. 1, e, f). They contrast sharply with the thick, coarse pappus setae of *Soroseris* (Fig. 1, c, d). On the basis of these differences the writer believes that this section of *Lactuca* has no particular relationship with *Soroseris*, but has acquired a similar habit through parallel evolution, in response to a similar environment.

The affinities of Sect. AGGREGATAE to other species of *Lactuca* are somewhat obscure. *L. macrorhiza* Hook. f. resembles *L. Souliei* Franch., the best known species of Sect. AGGREGATAE, in leaf shape, flower color, the character of the stigmas and to some extent the involucral bracts. The involucres of *L. macrorhiza*, however, have many more bracts and florets, while its involucral bracts are in several series, and more or less evenly imbricated. The corollas of *L. macrorhiza* and its relatives have short tubes and long ligules, while the achenes are either longer beaked or are not so abruptly contracted at the apex, and are more striate. In their heads with few florets and long corolla tubes the species of Sect. AGGREGATAE, approach those of Sect. SORORIA, but these two sections are very different in habit and in their achenes. The present section is therefore an isolated one, but has its nearest relatives among characteristic Sino-Himalayan species.

The three species may be identified by the following key:

A. Leaves lyrate-pinnatifid; achenes strongly obcompressed, 1-nerved on each face. 2. *L. Souliei*

A. Leaves merely dentate; achenes moderately obcompressed, 5-ribbed; ovary with 5 vascular bundles.

B. Leaves on slender, wingless petioles, closely sinuate dentate; corolla 16–19 mm long; anther tube 5–5.5 mm long; pappus setae 10–12 mm. . . . . 1. *L. porphyrea*

B. Leaves on short, alate petioles, remotely repand-dentate; corollas 8–9 mm long; anther tube 2–2.5 mm long; pappus setae 7–10 mm. . . . . 3. *L. disciformis*

1. **Lactuca porphyrea** (Marq. & Shaw) comb. nov. (Fig. 12, *e–f*)—Stems from a slender root, 5–6 cm long, expanded toward the apex; leaves purplish red, glabrous, on slender petioles which are expanded at the base to a triangular sheath, the blade elliptic to obovate or spatulate, closely sinuate-dentate; involucres 11–13 mm long; their bracts uniseriate, 4–5 in number; corollas purple, 16–19 mm long, the tube slender, 9–10 mm long; branches of the stigma pale, 2 mm long, 0.27 mm broad; achenes unknown; pappus setae 10–11 mm long. (*Crepis glomerata* var. *porphyrea* Marq. et Shaw, Jour. Linn. Soc. Bot. 48: 194, 1929.)

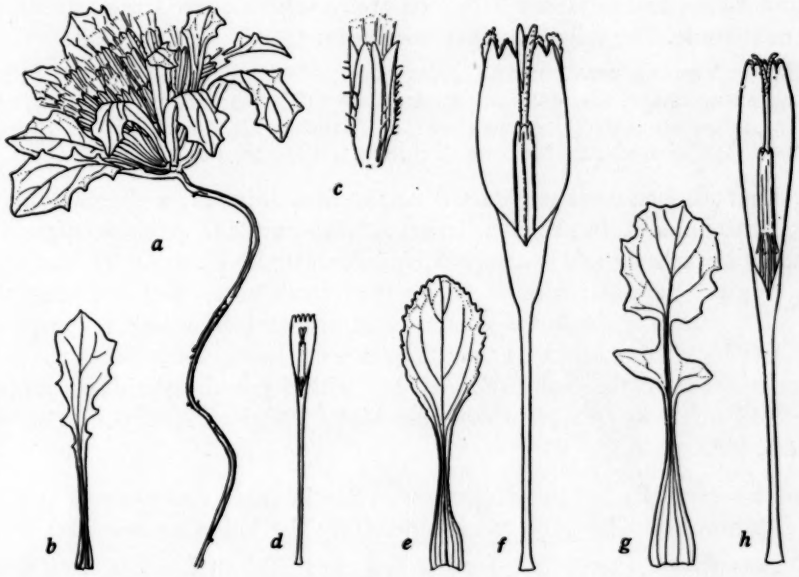

Fig. 12. *a–d*, *Lactuca disciformis*, from type (B): *a*, habit, ×1; *b*, leaf, ×1; *c*, involucre, ×2; *d*, corolla, ×4. *e–f*, *Lactuca porphyrea*, from type: *e*, leaf, ×1; *f*, corolla, ×4. *g*, *h*, *Lactuca Souliei*, from Schneider 3136 (US): *g*, leaf, ×1; *h*, corolla, ×4.

Known only from the type: TIBET: On bare stony chutes and screes, above Pasum Lake, alt. 3400–3600 m, *Ward 6113* (K, type). Also seen by the same collector above Atsa, 4850–5150 m (note on label of type specimen).

The distinctions between this species and *Soroseris glomerata* have already been mentioned in the discussion of the Sect. AGGREGATAE. The two species, although superficially similar in habit, are not related to each other. The collector of *L. porphyrea*, Capt. F. Kingdon Ward, identified correctly the genus of this plant, since the original label bears the legend "Lactuca sp." Furthermore, his keen eye for plants in the field was able to judge its true relationships. In describing the flora of Pasum Lake (Gard.

Chron. 78: 130–131, 1925) he says that he found "on some gravel screes, a fine, purple-flowered *Lactuca*—not the one which is so common in western China (presumably *L. Souliei*), but a much larger flowered species."

2. LACTUCA SOULIEI Franch. Jour. de Bot. 9: 257. 1895. (Fig. 12, *g–h*)—Leaves purplish or green, lyrate-pinnatifid, the lobes angulate-dentate; involucres 11–13 mm long, similar to those of *L. porphyrea;* corollas blue, 14–15 mm long, the tube 8–9, the ligule 6–7 mm long; anther tube blue, 4–4.5 mm long; stigma branches 1.5–1.8 mm long; achenes 4–4.5 mm long, reddish, strongly flattened, with 1 nerve on each face; pappus setae 8–9 mm long. Western China and adjacent Tibet, on stony talus slopes (screes) at 3300–4400 m altitude. The following have been seen:

CHINA: Yunnan prov., near Lichiang, alt. 4000 m, *Schneider 3136* (US); Likiang snow range, alt. 4400 m, *Rock 24886* (UC, K); near Chungtien, alt. 4000 m, *Schneider 3001* (US); northeast of Atuntze, alt. 4000–4250 m, *Forrest 20289* (US); Chien-chuan-Mekong divide, alt. 4200 m, *Forrest 23126* (US).

3. LACTUCA DISCIFORMIS (Mattf.) comb. nov. (Fig. 12, *a–d*)—Similar to the last two in habit, but smaller; leaves reddish-purple to greenish, spatulate to obovate, remotely and coarsely repand-dentate; involucres 9–11 mm long (excluding the pappus); corollas purple (collector's note), 8–9 mm long, the tube 5.5–6 mm, the ligule 2.5–3 mm long; anther tube bluish or purplish, 2–2.5 mm long; stigmatic branches 0.6 mm long; immature achenes reddish, similar in shape to those of *L. Souliei*, but with 5 prominent ridges; pappus setae 7–10 mm long. (*Crepis disciformis* Mattf., Notizbl. Bot. Gard. Berlin-Dahlem, 1935, p. 46.)

Southwestern Kansu and northwestern Szechuan, in rocky places and alpine meadows, at 4000–5100 m altitude. Only the following has been seen.

CHINA: Kansu Prov., Mt. Kwang Kei, west Tebbu Land, alt. 4000 m, *Rock 13729* (B type, US).

This species is in the reduced size and the proportions of its corollas farther removed from *Soroseris* than are the other two species of the section AGGREGATAE. In every important diagnostic characteristic except the 5-costate achenes it resembles *L. Souliei.*

VI. DISTRIBUTION OF THE SPECIES

A. DUBYAEA

According to our present knowledge, the species of *Dubyaea* show a remarkably high degree of endemism. The genus itself is endemic to the Sino-Himalayan region, while six of its nine species are highly localized, even within that area. Seven species are endemic to western China or southeastern Tibet, one to the northwestern Himalaya, while one, *D. hispida*, occurs in both the Chinese mountains and the Himalaya (Fig. 13).

There are no endemic species of *Dubyaea* known from the eastern Himalaya. Another remarkable fact is that three species, *D. chimiliensis*, *D. gombalana*, and *D. amoena*, are known only from a single series of mountain ranges, those forming the divide between the Salween and Irrawady river systems, while a fourth, *D. tsarongensis*, is nearly confined to these ranges. In addition, it is interesting to note that the only two species which are not alpine or subalpine in their distribution, *D. oligocephala* and *D. glaucescens*, occur at opposite ends of the range of the genus, the former in the northwestern Himalaya, the latter in Szechuan.

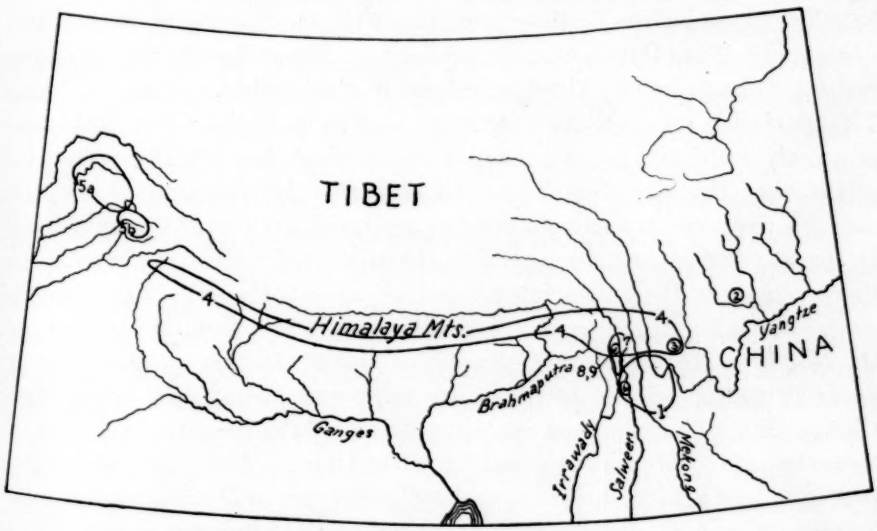

Fig. 13. The distribution, generalized, of the species of *Dubyaea:* 1, *D. atropurpurea;* 2, *D. glaucescens;* 3, *D. rubra;* 4, *D. hispida;* 5a, *D. oligocephala* subsp. *typica;* 5b, *D. oligocephala* subsp. *latifolia;* 6, *D. chimiliensis;* 7, *D. tsarongensis;* 8, 9, *D. amoena* and *D. gombalana.*

The above facts, coupled with our knowledge of the primitiveness of the species have a definite bearing on the interrelationships of the floras of which the species of *Dubyaea* form a part. Two hypotheses have been advanced as to the origin of the Sino-Himalayan flora. Diels (1913) has suggested that the alpine flora of China, like its temperate flora, is a very ancient one, and that the flora of the Himalaya is largely tributary to it. Ward (1935), on the other hand, believes that the Tertiary alpine flora of southeastern Asia was completely exterminated during the Pleistocene ice age, and that the present flora, including the various endemic genera, has originated in southeastern Tibet in post-Pleistocene time. The explanation of Diels obviously is much more in accord with the evidence from

Dubyaea. At least some of its species, *D. atropurpurea*, *D. hispida*, *D. oligocephala*, and *D. chimiliensis*, are clearly more primitive than, and probably older than the species of such widespread genera, as *Prenanthes*, *Lactuca*, and *Crepis*, which are themselves most certainly of Tertiary age (see below). Furthermore, most of the species of *Dubyaea* are very distinct from each other; if they had originated in recent times their phylogenetic interrelationships should be much clearer. Two of them could, perhaps, be of recent origin. *D. tsarongensis* is closely related to *D. chimiliensis*, and may have originated from it relatively recently, while *D. rubra* shows a similar relationship to *D. hispida*. The other species, however, appear to be relict types, whose Tertiary ancestors were much more numerous and widespread. Ward (1935) has produced convincing evidence that the alpine regions of southeastern Tibet were heavily glaciated in Pleistocene time. This glaciation may well have been the final catastrophe which destroyed or greatly restricted the species of a genus which had already passed its prime when the glaciation began. Of the few survivors, only *D. hispida* was able to spread extensively into the glaciated territory. *D. chimiliensis*, *D. amoena* and *D. atropurpurea* are, therefore, relict endemics similar to those found in the unglaciated nunatak areas of northeastern North America, Alaska, the Alps, and probably most of the mountain systems of the Northern Hemisphere. *D. glaucescens*, one of the two species found at lower altitudes, belongs to the warm temperate forest flora of western China, a flora characterized by "nine-tenths of the monotypic genera of trees that are so prominent a feature of the Chinese flora" (Wilson, 1929, p. 283). These genera, including such isolated types as *Davidia*, *Eucommia*, *Tapiscia*, *Carrieria*, *Itoa*, and *Idesia*, as well as the numerous genera in the same flora which have the well known distribution of Eastern Asia—Eastern North America (Wilson, 1929, p. 289), are certainly ancient, relict types, and probably represent the remnants of a flora which was widespread in Mesozoic and early Cenozoic time (Fernald 1931, p. 62). The presence of *D. glaucescens* in this assemblage, together with its isolated position both systematically and ecologically, suggests that its ancestors were also widespread at that remote period, and have since been superseded by their younger relatives in *Prenanthes*, *Lactuca*, *Crepis*, and *Hieracium*.

D. oligocephala also occupies an isolated range with respect to the other species of *Dubyaea*. It is interesting to note that the flora of the Northwestern Himalaya, where *D. oligocephala* is found, contains many European and Western Asiatic types not found elsewhere in the Sino-Himalayan region (Hooker 1909). That this is true of the tribe Cichorieae is

evidenced by the presence in that region of five species of *Hieracium* and of *Chondrilla*. Both of these are typically European and western Asiatic genera which are sparingly or not at all represented farther east. In view of this geographic affinity, the fact that *D. oligocephala* is more closely related than is any other species of *Dubyaea* to the predominantly European and western Asiatic genus *Crepis* has some significance. *D. oligocephala* may easily be the remnant of a group of species which was formerly widespread in Western Asia and Europe, and which figured in the ancestry of *Crepis*.

The distribution of *Dubyaea* agrees in general with that of another Composite genus, *Cremanthodium*. Good (1929) has given us a very thorough account of the distribution of this genus in relation to the climatic and physiographic features of the Sino-Himalayan region, and his account of the latter features serves very well as a guide to the distribution of *Dubyaea*. There is in both genera a concentration of species in the river gorge area of southeastern Tibet, northwestern Yunnan, and southwestern Szechuan. In both genera the number of endemics in the Himalaya is small. The same arguments, therefore, which are used by Good to indicate the origin of *Cremanthodium* prior to the Himalayan uplift hold also for *Dubyaea*. In addition, it is interesting to note that the eastern continuation of the Himalaya, the importance of which as a rain screen and consequently as a barrier to plant migration has been emphasized by Ward (1935), appears to have been important in limiting the range of three species. *Dubyaea atropurpurea* and *D. chimiliensis* occur only south of this barrier, while *D. hispida* has been found in this region only to the north of it. The fact that *D. atropurpurea* and *D. chimiliensis* are in their floral anatomy among the most primitive species of the genus (see below), and are furthermore unspecialized in habit, suggests that they are also the oldest, while *D. hispida* in these respects suggests a more recent origin. The fact that the two presumably older species are confined to the moist side of the rain screen is in accord with the suggestion of Good (1929, p. 314), that "before the Himalayan uplift . . . the western Chinese mountains were, except in the southwest, much wetter than now." Presumably *D. atropurpurea* and *D. chimiliensis* were more widespread at this early period than now, but were already so fixed that they could not adjust themselves to a changing environment, and so became confined to regions of which the climate was relatively little affected by the Himalayan uplift. *D. hispida*, on the other hand, probably originated since the beginning of the Himalayan uplift, and has apparently been increasing its range in relatively recent times.

B. SOROSERIS

The genus *Soroseris* is endemic to the same general region as the related genus *Dubyaea*, but the distribution of the species within this region is quite different. The eight species, as recognized in the present treatment, are distributed as follows (Fig. 14). Two, *S. rosularis* and *S. bellidifolia*, are known only from western China; one, *S. Deasyi*, occurs in the northwestern Himalaya and adjacent western Tibet; one, *S. glomerata*, in south central Tibet and the west central Himalaya, and one, *S. pumila*, in the eastern Himalaya. The three more widespread species are all found in

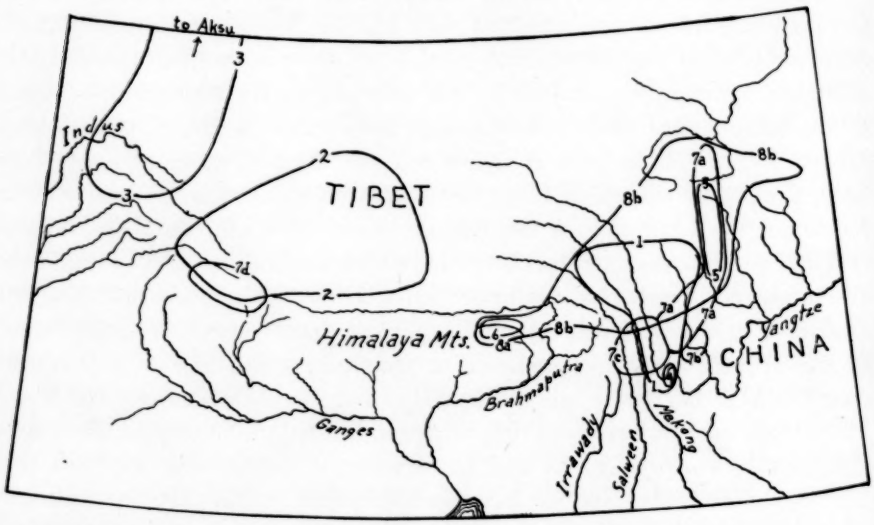

Fig. 14. The distribution, generalized, of the species of *Soroseris:* 1, *S. umbrella;* 2, *S. glomerata;* 3, *S. Deasyi;* 4, *S. rosularis;* 5, *S. bellidifolia;* 6, *S. pumila;* 7a, *S. Gillii* subsp. *typica;* 7b, subsp. *Handelii;* 7c, subsp. *hirsuta;* 7d, subsp. *occidentalis;* 8a, *S. Hookeriana* subsp. *typica;* 8b, subsp. *erysimoides.*

southeastern Tibet. One of these, *S. umbrella*, extends eastward to the mountains of Szechuan and Yunnan, and west to the eastern Himalaya. Another, *S. Gillii*, also extends eastward to Szechuan and Yunnan, where it is more common than *S. umbrella*, but skips the eastern Himalaya, recurring in Kumaon and Garwhal, in the west-central Himalaya. The third, *S. Hookeriana*, is the most widespread species of all. It also extends to the mountains of China, but has a more northerly range there than *S. umbrella* and *S. Gillii*, and is in addition the most common species of *Soroseris* in the eastern Himalaya.

When this distribution is compared with that of *Dubyaea*, two striking differences are evident. In the first place, the species of *Soroseris* have, in

general, a much wider distribution than those of *Dubyaea*. The only two species whose known range is relatively restricted are *S. rosularis* and *S. pumila*. *S. rosularis*, moreover, is doubtfully distinct from *S. bellidifolia* and *S. Deasyi*. The remaining six species all have as broad or broader ranges than any species of *Dubyaea* except *D. hispida*. The second difference is that the species of *Soroseris* are not concentrated in the Chinese mountains as are those of *Dubyaea*. The only two species not known west of longitude 98° are *S. bellidifolia* and *S. rosularis*. As is stated in the systematic section of this paper, these two species are doubtfully distinct from each other and from *S. Deasyi*, of Kashmir, western Tibet, and Turkestan. These three forms may, when further material has been seen, prove to be merely geographical segregates of one widespread species of which the center of distribution is in Tibet. If this proves to be true, then every species of *Soroseris* will be represented in the Tibetan flora. For this reason, the writer believes that the Tibetan plateau is the center of distribution of *Soroseris*. In contrast to this, the present center of *Dubyaea* is the mountains of southwestern China, and of the river gorge region in the southeastern corner of Tibet. The definite affinity between *Soroseris* and *Dubyaea* is in full agreement with the opinions of Hemsley and Pearson (1902), and Ward (1935), that the greatest affinity of the Tibetan flora is with that of the Sino-Himalayan region.

One of the interesting features of the distribution of *Soroseris* is the presence of two forms in the western Himalaya which have their closest relatives in the Chinese mountains but not in the eastern Himalaya. The affinity of the northwestern Himalayan *S. Deasyi* to *S. rosularis* of Yunnan has already been mentioned; *S. Gillii* subsp. *occidentalis* of Garwhal Kumaon, and adjacent Tibet is the second case. This affinity between the Chinese mountains and the western Himalaya has been shown by Diels (1913) to exist in a number of genera.

VII. FLORAL ANATOMY OF DUBYAEA AND SOROSERIS

A wealth of evidence obtained from many different groups has shown that the vascular anatomy of the flowers provides valuable clues to the interrelationships and phylogeny of families, genera and species of Angiosperms. *Dubyaea* and *Soroseris* have proved particularly interesting among the genera of the Cichorieae in this respect, and for this reason the floral anatomy of their species will be described in some detail. Since no preserved flowers of either *Dubyaea* or *Soroseris* were available, this study was of necessity based entirely on preparations obtained from herbarium specimens. They were made in two ways. Whole mounts of florets of all of the species were prepared according to the bleaching and clearing

method devised by the author (Stebbins 1938). In addition, material of the more critical species was boiled in water for 20 minutes, then soaked in hot water in a double boiler for 2–3 hours, after which it was transferred first to 95% ethyl alcohol, then to butyl alcohol. It could then be embedded in paraffin, sectioned, and stained in gentian violet according to the usual schedule. The preparations thus obtained, though somewhat crushed in places, were well stained, and showed the position of the vascular bundles very clearly. For the sake of comparison, sections of florets, of *Prenanthes trifoliolata* (Cass.) Fernald, which in general resembles *Soroseris* in its floral anatomy, were also studied. The only advantage of these sections for anatomical study over those obtained of *Dubyaea* and *Soroseris* lay in their more reliable preservation of the more delicate tissues, such as the phloem. The author feels confident, therefore, that the description given below is quite accurate as to the general features which it includes, even though it is not based on the usual well preserved material.

The floral anatomy of several species of Compositae, including one species of the tribe Cichorieae, *Lapsana communis*, was thoroughly investigated by Koch (1930a, b). Although the species of *Dubyaea* and *Soroseris* agree in general with her descriptions, most of them have certain striking features not described by her. These features provide valuable evidence bearing not only on the position of these two genera in the tribe Cichorieae, but in addition on the broader relationships of the tribe and perhaps the Compositae as a whole. These features all involve the anatomy of the ovary, style, and stigma; the corollas of all of the species agree with the description given by Koch (1930a) of *Lapsana*, and which has been found by the present writer in practically every species of Cichorieae investigated. A slight exception is found in *Dubyaea atropurpurea*, in which the median bundles of the corolla lobes (cf. Koch 1930a) exist at its apex and extend down to about the base of the teeth, where they disappear.

The species of *Dubyaea* are remarkably diverse in the anatomy of their ovaries, since among the nine known members of this genus five different anatomical types are found. Three species, *D. atropurpurea*, *D. chimiliensis*, and *D. gombalana* are interesting enough to be described in detail.

D. atropurpurea (Fig. 15, *a–h*). At the base of the ovary of this species five large bundles pass out from the stele (Fig. 15*a*). Since these eventually form the supply to the corolla, stamens, and style, they are termed the principal bundles. Directly above this level the stele divides into a varying number of lesser bundles, leaving only a small remainder of vascular tissue in the center. These lesser or supernumerary bundles pass directly out between the principal bundles to the ovary wall (Fig. 15*b*). Some of them

then form two or three branches, while others remain unbranched. All are much smaller than the principal bundles, and become differentiated at a later stage. They are best seen in ovaries from which the corolla has withered, and which have begun to grow into achenes. The remainder of the vascular tissue forms the ovule trace, which is at first rather broad and is embedded in a large mass of parenchyma. At the base of the cavity of the ovary, this parenchyma separates into two ribbon-shaped bands which pass toward the ovary wall on either side of the ovule trace and then turn upward, so that they appear crescent-shaped in cross section (Fig. 15*c*). They soon become narrower, and are differentiated into clearly recognizable, though relatively weakly staining, xylem and phloem elements. The differentiation of these two inner bundles takes place last in the development of the ovary; in all of the species examined they were not completely differentiated until well after flowering time. They are the conducting cords of other authors (Lavialle 1912). They continue on either side of the ovule until slightly above its summit, so that a cross section of the ovary at this level (Fig. 15*d*) shows an outer row consisting of the 5 principal and 7–10 or more supernumerary bundles, and an inner pair of relatively indistinct, flattened ones. The latter now disappear. At the apex of the ovary the central cavity becomes cruciform in outline, with the ends of two of the arms directly over the position of the inner pair of bundles (Fig. 15*e*).The principal bundles have become much broader, while most of the supernumerary bundles drop out at this point. Four of the principal bundles then give rise to bundles supplying the style (Fig. 15*f*). Two of these are relatively thick; they arise at a slightly lower point than the other two, and pass diagonally upward and inward along the long axis of the ovary. The other two more slender ones pass horizontally inward, or may even turn downward slightly. They reach the edge of the much reduced ovary cavity, which has now become elongated parallel to the short axis of the ovary, directly over the position of the two inner bundles, where they turn abruptly upward to enter the style. The stamen bundles diverge from those of the corolla at nearly the same level at which the stylar bundles branch inward from the principal ones. The four stylar bundles continue upward to the base of the stigmatic branches, where the two lesser ones divide, sending one branch to each of the two stigmas. Each stigmatic branch, therefore, contains three bundles; a strong central one and two smaller lateral ones (Fig. 15*h*).

D. chimiliensis (Fig. 15*g*). This species is similar to *D. atropurpurea* except for three differences. The supernumerary bundles are relatively few in number (3–5), are not branched, and sometimes end below the summit of the achene. The two inner bundles are connected with the summit

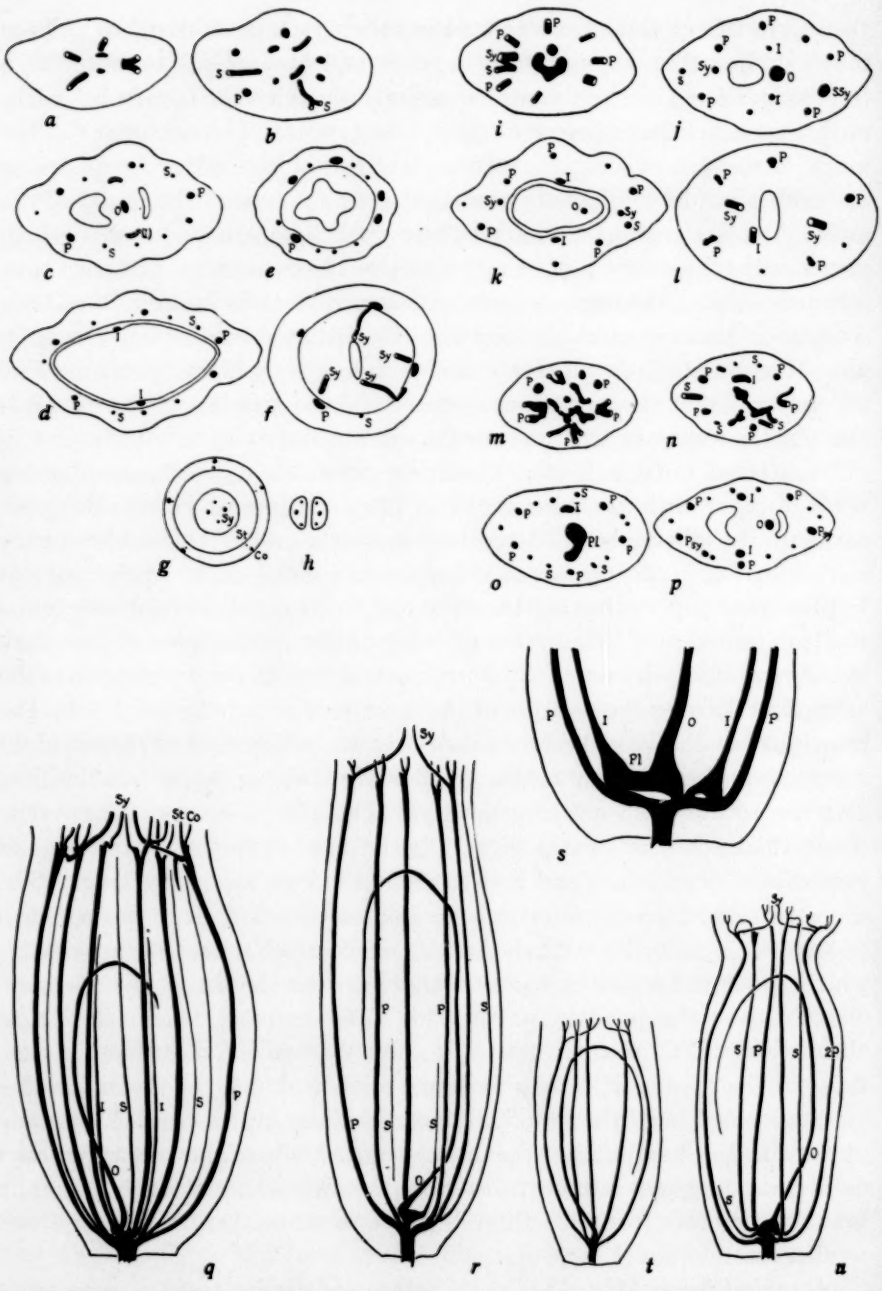

Fig. 15. *a–h*, Diagrams of cross sections at successive levels of the mature ovary of *Dubyaea atropurpurea*. *a*, base of ovary, showing principal bundles passing out from stele; *b*, slightly higher level, showing supernumerary bundles (S) passing out between the principal ones (P); *c*, base of ovary cavity, showing principals, supernumeraries,

of the stele, emerging on either side of the ovule trace, as described below for *D. gombalana*. Finally the two lesser stylar bundles end just below the base of the stigmas, so that the stigmatic branches themselves contain only one bundle each.

D. gombalana (Fig. 15, *i–l*). In this species the supernumerary bundles are as in *D. chimiliensis*, except that they pass out from the stele at practically the same level as the principal ones, and members of the two series are often fused for a short distance. The remainder of the stele exists for a short distance as a nearly continuous ring (Fig. 15*i*), then breaks up into the large ovular trace and the two inner bundles, one of which leaves the stele slightly before the other (Fig. 15*j*). These two inner bundles extend farther up the ovary than in *D. chimiliensis* or *D. atropurpurea*, and in the specimen illustrated one of them has persisted to the apex of the ovary (Fig. 15*e*), where it occupies a position comparable to that of the lesser stylar bundles in *D. atropurpurea* (cf. Fig. 15*f*). It ended at this point, however, and the style of *D. gombalana* has only two bundles, corresponding to the larger ones in *D. atropurpurea*. The course of these stylar bundles, however, differs strikingly from the situation in *D. atropurpurea* and *D. chimiliensis*. One or both of them are free from the principal bundles throughout almost their entire length. They branch off from one of the principal at about the level of the base of the ovary cavity, and continue upward near the inner edge of the ovary wall. The middle part of the

---

ovular bundle (O), and parenchyma from which inner bundles arise (I); *d*, upper part of ovary, above apex of ovule, showing principals, supernumeraries, and inner bundles; *e*, near summit of ovary, showing expansion of principal bundles and cruciform shape of cavity; *f*, summit of ovary, showing stylar bundles (Sy) passing inwards; *g*, base of corolla, showing corolla (Co), stamen (St), and stylar (Sy) bundles; *h*, cross section of stigmatic branches showing three bundles in each branch. *i–l*, diagrams of cross sections of ovary of *Dubyaea gombalana*, *i*, base of ovary, showing principal and supernumerary bundles, and central mass of vascular tissue; *j*, base of cavity; one of the stylar bundles is free, the other still fused to a supernumerary bundle; the large ovular and the two inner bundles are evident; *k*, middle of ovary, showing principal, supernumerary, stylar, and inner bundles; *l*, summit of ovary; stylar bundles passing inward, one inner bundle still evident. *m–p*, *Soroseris Deasyi*; *m*, base of ovary; *n*, next section above, showing one inner bundle and irregular mass of vascular tissue in center; *o*, slightly higher section, showing placental platform (Pl); *p*, base of ovary cavity, showing ovular and enlarged inner bundles; Psy, the two principal bundles from which the stylar bundles will arise. *q*, *Dubyaea chimiliensis*, diagram of vascular system of ovary; P, principal; S, supernumerary; O, ovular; I, inner; Co, corolla; St, stamen; Sy, stylar bundles. *r*, *Dubyaea hispida*, vascular system of ovary. *s*, *Soroseris Gillii*, Diagram of median longitudinal section at base of ovary; *t*, *Crepis nana*, showing reduced vascular system of ovary most frequent in the Cichorieae; *u*, *Lactuca Lesserti-ana*, showing fusion of two principal bundles (2P).

ovary in cross section, therefore, shows an outer series of 7–9 and an inner one of 4 bundles (Fig. 15*k*).

D. oligocephala and *D. tsarongensis* are similar to *D. gombalana*, except that the inner bundles are less strongly developed, and one or both of the stylar bundles are adnate to the principal ones. *D. hispida*, *D. amoena*, and probably *D. rubra* are also similar, except that the stylar bundles are always both adnate to the principals (Fig. 15*r*). *D. glauscens* lacks the supernumerary bundles, so that its anatomy is essentially like that illustrated by Koch (1930a) for *Lapsana communis* and by the present author (Fig. 15*t*) for *Crepis nana*. Thus there exists within *Dubyaea* a complete series of anatomical types illustrating the reduction from the complex structure found in *D. atropurpurea*, *D. chimiliensis*, and *D. gombalana*, to the simple type which is probably the most common one in the Cichorieae as a whole.

The species of *Soroseris*, on the other hand, are much more uniform anatomically, and all conform to the pattern exemplified by *S. Deasyi* and *S. Gillii* subsp. *typica* (Fig. 15, *m–p*). In these the supernumerary bundles are relatively numerous, but pass out of the stele at practically the same level as the principal ones, the two series often being fused at the base (Fig. 15*m*). There remain in the center several irregular masses of vascular tissue, which quickly form themselves into two groups. One of these is the much broadened base of one of the two inner bundles, while the other is a large platform of vascular tissue, crescent-shaped in cross section (Fig. 15*o*). From one end of this platform there emerges the second inner bundle, while at the other, in the center of the ovary, is the ovule trace. This is much thickened at the base, and gradually tapers upward (Fig. 15*p*, *s*). The inner bundles become quickly weaker, and in the middle of the ovary are flattened, weakly staining strands like those of *Dubyaea atropurpurea*, which die out in its upper portion. The principal and supernumerary bundles continue to the summit of the ovary, where the former give rise to 2 stylar, 5 corolla, and 5 stamen bundles, and the latter end, as in *Dubyaea hispida*. The species of *Soroseris*, therefore, resemble *Dubyaea atropurpurea* in the number of their supernumerary bundles, but are more like *D. gombalana*, *D. hispida*, and many other species in the fusion of the bases of principals and supernumeraries, and in the number of stylar bundles, while they suggest *D. gombalana* in the strong development of the inner bundles. A striking feature of the anatomy of *Soroseris*, not found in any species of *Dubyaea*, is the large, thick platform of solid vascular tissue (mostly xylem elements) from which the ovule trace and one of the inner bundles arise (Fig. 15*p*, *s*).

Interpretation of Floral Anatomy

Due to the great degree of reduction, fusion, and adnation found in the Compositae, the interpretation of the homologies of the various vascular bundles described above is difficult. For this reason, they have been described as objectively as possible, without designating them by names which would imply their homologies. These homologies, however, can be inferred with some assurance on the basis of the whole series of forms investigated, together with the results obtained by other workers, principally Dr. Koch, and on the available knowledge of the situation in other families.

In the first place, the principal and supernumerary bundles apparently belong respectively to an outer and an inner whorl of perianth members, that is the calyx and corolla. This assumption can be reconciled with the fact that the outer, or principal series actually supplies the corolla when we remember that the only bundles persisting in the corolla of the Cichorieae are those leading to the sinuses between the lobes. These bundles as Koch has pointed out, represent the fused lateral bundles of two adjacent petals, and normally would be opposite the calyx lobes. With the adnation of calyx and corolla, therefore, these fused laterals would tend to fuse with the median sepal bundles directly opposite them. The principal bundles, therefore, probably represent the median sepal bundles, to which have been fused the lateral corolla as well as the stamen bundles. On this basis the supernumerary bundles, which apparently correspond to the "vestigial bundles" found by Koch (1930a) in *Solidago nemoralis*, must represent the median corolla bundle system, which persists only in that part of the corolla limb adnate to the ovary, and in *Dubyaea* and *Soroseris* never extends upward into the free, visible part of the corolla. This interpretation is strengthened by the evidence from *Senecio cruentus* DC. In this species the ovary of the disk florets has 5 primary and 3–5 supernumerary bundles. The latter arise much as they do in *Dubyaea glomerata* and *D. hispida*. In some cases they die out in the upper part of the ovary wall, as in the Cichorieae, while in others they continue into the corolla, and extend to the apex of a lobe, thus forming a median corolla bundle.

The two major bundles supplying the style in *Dubyaea atropurpurea* and *D. chimiliensis*, and the only two stylar bundles present in the other species, represent the dorsal carpellary bundles, as is generally true of Angiosperms. (Eames 1931, Hunt 1937). These are adnate to the composite median calyx-lateral corolla-stamen bundles except in *D. gombalana* and in some ovaries of *D. oligocephala* and *D. tsarongensis*. There remains the problem of the lesser stylar bundles and of the two inner bundles or con-

ducting cords. Their homology presents a dliemma, since both of them give evidence of representing the ventral carpellary bundles. The lesser stylar bundles in *D. atropurpurea* form the lateral bundles of the stigmatic branches, conforming exactly to the diagram of Eames (1931, Fig. 29*c*), and agreeing with the interpretation of Hunt (1937) that the stigma or stigmatic branch, when it possesses three veins, represents the apex of a much contracted and narrowed, but primitively trilobate sporophyll, of which the lateral lobes are supplied by the ventral carpellary bundles, which bundles also supply the placentae. On the other hand, the close connection between the base of one or both of the inner bundles and the ovule trace in *Dubyaea gombalana*, *D. chimiliensis*, and the species of *Soroseris* suggests that these bundles are the placental ones, and therefore the ventral carpellary bundles. This interpretation seems particularly apt in the case of *Soroseris*, in which the ovule trace appears to arise from the much broadened and thickened base of one of these two bundles, while the other arises from a different part of the apex of the stele (Fig. 15*s*). Further evidence for it is the fact that both of the inner bundles, when well developed, are much broadened at the base, in marked contrast to the other bundles of the ovary. This broadening may very well represent a vestigial placental surface, from which, in the many-ovuled ancestors of the Cichorieae, additional ovule traces arose.

An hypothesis to explain this difficulty is suggested by the fact that the lesser stylar bundles, when present, always pass into the stigma at a point directly above the position of the two inner bundles. Perhaps, therefore, both sets of bundles represent portions of the ventral carpellaries, which in the ancestral form were continuous from the base of the ovary into the style, but which during the phylogenetic process of reduction have disappeared from the upper part of the ovary. Before this disappearance the upper portion of the ventral carpellary bundles was connected to a median lateral carpellary (Eames 1931, p. 156) by means of a short horizontal bundle, such as is usually found in well developed carpels as part of the netted venation of their walls. The fusion of the median lateral with a primary calyx-corolla bundle and the disappearance of the ventral in the upper part of the ovary resulted in the apparent fusion of the upper part of the ventral bundle to a principal. The secondary nature of the horizontal basal portion of the lesser stylar bundles is strongly suggested by their irregular course, and by the irregular shape of their tracheids. Furthermore, they always pass inward diagonally, so that the lesser stylar bundles are never opposite the principals to which they are connected.

If this hypothesis is correct, then some form should be found, either among the primitive Compositae or their relatives, in which ventral

bundles situated like those of *Dubyaea* and *Soroseris* are continuous, and possess the horizontal connecting bundle at the summit of the ovary. This situation is approached in the specimen of *D. gombalana* illustrated in Figure 15*l*.

The type of ovary ancestral to that now found in the Cichorieae was therefore, probably bicarpellate but unilocular, with two parietal placentae formed by the fused ventral bundles of adjacent carpels corresponding to the diagram of Eames (1931, fig. 29). Furthermore, the lack of adnation, so far as the vascular system is concerned, between ovary and perianth in *D. gombalana* suggests that the Cichorieae are not very distantly related to ancestral forms possessing a superior ovary. Koch (1930a, b) did not report this condition in any of the species investigated by her. The writer has seen it as an occasional feature in the florets of *Senecio cruentus* DC., *Ligularia japonica* (Thunb.) Less., and *Cremanthodium Helianthus* Maxim., and a few other species of the *Senecioneae*, and in *Dinoseris salicifolia* Griseb. of the Mutisieae, but it is by no means common in the Compositae, and the writer knows of no species in which it is as regular a feature as in *Dubyaea gombalana*. A fuller discussion of these points in connection with the phylogeny of the Cichorieae as a whole will be presented in a later publication.

Comparison with other genera of Cichorieae

There are no other genera known to the writer in the Cichorieae which contain as many primitive anatomical features as *Dubyaea* and *Soroseris*. The nearest approach to the situation found here is in *Prenanthes*. In most of the species of this genus (*P. purpurea* L. and *P. yakoensis* Jeffr. are exceptions) supernumerary bundles are present. They may be few, as in *Dubyaea hispida*, or numerous, as in *Soroseris*. The latter situation is most characteristic of the American species of *Prenanthes* (*P. serpentaria* L., *P. alba*, L., *P. trifoliolata* (Cass.) Fernald, *P. altissima* L.) but occurs also in the Asiatic *P. acerifolia* (Maxim.) Matsum. In all of the species of *Prenanthes* there are only two stylar bundles, that is the dorsal carpellaries, but in *P. acerifolia* one or both of these may be free from the calyx-corolla, principal bundles. The "platform" of vascular tissue that is so conspicuous in *Soroseris* exists also in *Prenanthes*, although its shape is somewhat different in the latter genus, while the two inner, presumably ventral carpellary bundles occur regularly in the developing achenes.

Youngia, Sect. DESIPHYLUM, also approaches *Dubyaea* and *Soroseris* anatomically. *Y. depressa* (Hook. f.) Babcock & Stebbins and *Y. conjunctiva* Babcock & Stebbins, the two species of this section investigated, both have supernumerary bundles and well developed platforms. In *Y. con-*

junctiva four bundles are generally present in the style although in both species the stylar bundles are adnate to the principal calyx-corolla series. The material available was not old enough for the determination of the presence or absence of the inner "ventral" bundles. In the remaining sections of *Youngia* and in the related *Ixeris* the *Lapsana* type of anatomy is predominant. *Crepis*, also, has a more reduced floral anatomy than the more primitive species of *Dubyaea*. Supernumerary bundles occur in some species of the subgenus CATONIA and in a few of EUCREPIS, while in *C. aurea* (L.) Cass., *C. mollis* (Jacq.) Asch. and perhaps a few other species one of the dorsal carpellaries is occasionally free from the primaries. Three or four stylar bundles exist in *C. paludosa* (L.) Moench., *C. viscidula* Froel., and *C. geracioides* Haussk. The two "ventral" bundles have been seen in *C. occidentalis* Nutt. and probably occur in other species. The majority of *Crepis* species, however, have the simple *Lapsana* type of anatomy, as exemplified by *C. nana* Richards. (Fig. 15*t*). Only twelve species of *Hieracium* have as yet been examined, but all of these had the *Lapsana* type of anatomy except for *H. umbellatum* L. and *H. Nakaii* Kitagawa. In the former species one of the dorsal carpellaries was free in about one-half of the ovules of a specimen from Blankenburghe, Belgium, but no supernumerary bundles were found, while in *H. Nakaii* the dorsals are adnate but supernumeraries occur. The species of *Lactuca*, except for a few exceptional ones like *L. porphyrea* and *L. disciformis* (see above), have two or more of the principal bundles fused, so that the number of these bundles is reduced to four, three, or most often two (cf. Stebbins 1937). Supernumerary bundles are present in a few species, such as *L. Lessertiana* (Fig. 16*u*), but are usually lacking. *Lactuca*, therefore, has the most specialized floral anatomy of any of the genera under consideration.

VIII. SOME HISTOLOGICAL CHARACTERISTICS OF DUBYAEA AND SOROSERIS

Two histological characteristics are of value in determining the relationships of *Dubyaea* and *Soroseris*. These are the presence or absence of sclerenchymatous tissue at the summit of the ovary, and the form of the crystals found in the uppermost part of the ovary wall. Both of these can be determined from herbarium specimens. They are quite evident in the cleared mounts of ovaries which were used for anatomical study, and can be determined on any herbarium specimen by boiling ovaries first in water, then in concentrated ammonia on a slide, and then flattening them out under a cover glass.

The sclerenchymatous tissue, when present, usually covers the summit of the ovary, in the region inside of that occupied by the vascular bundles which supply the corolla (Fig. 16*e*). Its cells are large, thick-walled,

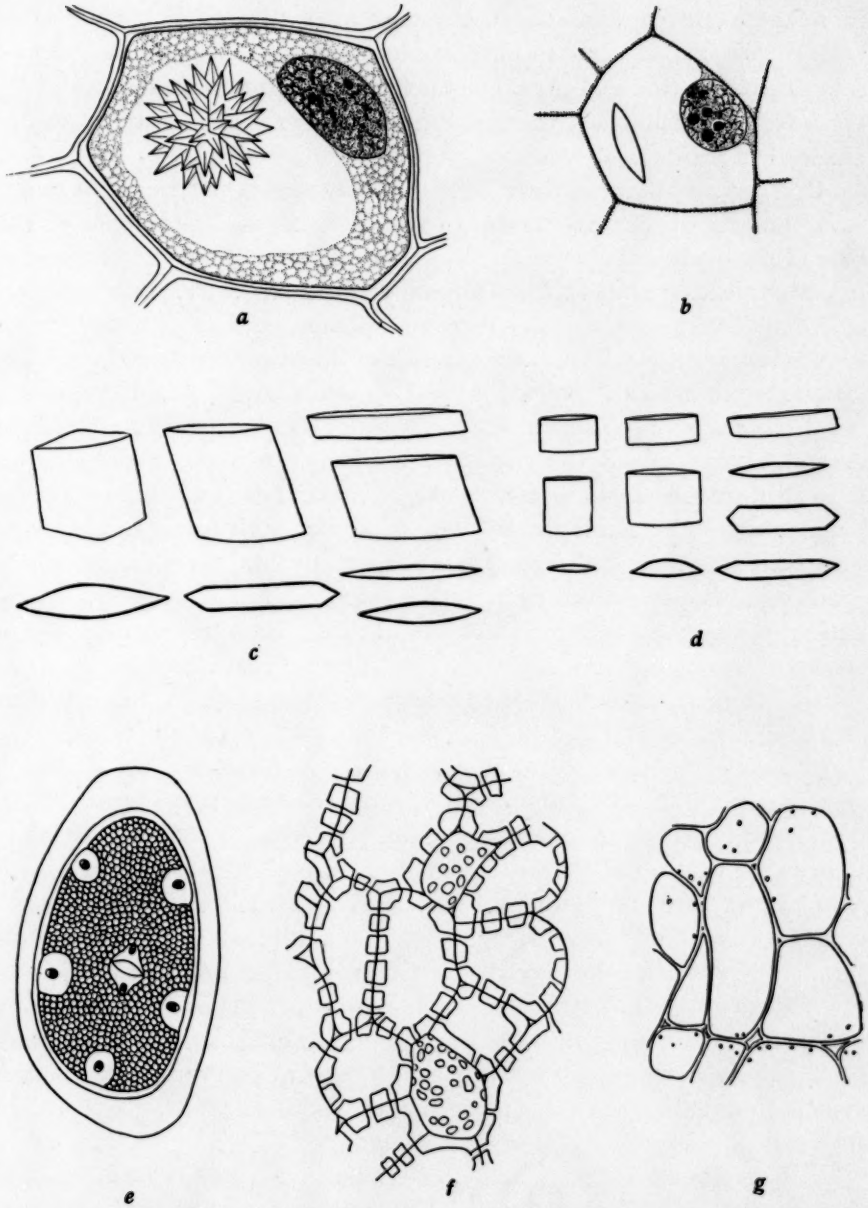

Fig. 16. *a–d*, Types of crystals: *a*, cell from ovary wall of *Crepis intermedia; b*, cell from ovule integument of the same; *c*, crystals from summit of ovary of *Dubyaea oligocephala; d*, from ovule integument of the same. All ×1250. *e*, Diagram of summit of ovary of *Soroseris Deasyi*, showing position of sclerenchyma (circles). *f*, sclerenchyma cells from *S. Deasyi; g*, parenchymatous cells from the corresponding region of *Dubyaea chimiliensis.*

prominently pitted, and stain the same color as the xylem strands (Fig. 16f). In contrast, the cells in the same region of such a species as *Dubyaea chimiliensis* are thin-walled and parenchymatous. Intermediate conditions are sometimes found, but the lignified sclerenchyma can always be recognized when present.

Crystals may occur in three regions in the ovary; the apex of the ovary wall, the base of the same, and the ovule integument. Those found at the base of the ovary are always the same as those at its summit, but the ones in the ovule integument are usually different in structure. Both types reacted positively to the usual tests for calcium oxalate (Ballard 1921). Figure 16*a* shows a cell from the summit of the ovary of *Crepis intermedia* Gray, containing an aggregate crystal, or druse, while Fig. 16*b* shows a cell from the ovule integument of the same floret containing a simple crystal, shown in end view. Both cells were drawn from a preparation fixed in a chrome-acetic formalin fixative, sectioned, and stained with a modification of Flemming's triple stain. The crystals found in the ovule integument of *Dubyaea oligocephala* are exactly like those in the corresponding tissue of *Crepis*, while in the ovary wall of *D. oligocephala* the same type of crystal is found (Figs. 16*c*, and *d*). These simple crystals are strongly flattened, being narrowly lenticular or prismatic in end view, and rectangular, rhomboidal, or occasionally pentagonal or hexagonal in side view.

The type of crystal found in any tissue is in these species apparently correlated with the condition of the cytoplasm at the time of crystallization. Both types are undoubtedly formed within the cytoplasm, and come to lie in the vacuole only after the cell has matured. In the cells which form aggregate crystals, the cytoplasm is relatively dense and evenly distributed while the crystal is forming, while the simple crystals are apparently formed in cells which have relatively thin cytoplasm, and in which vacuoles appear early. The structure of the crystals, therefore, is a significant indicator of certain physico-chemical properties of the cells in which they occur. The specificity of their occurrence both as to types of tissue and groups of organisms is clearly pointed out in Netolitzky's (1927) thorough review of the subject.

Table I shows the distribution of sclerenchyma and crystal types in the eight genera under consideration. In this table, the presence of sclerenchyma is indicated by a + sign; its absence by a − sign. The letter a denotes aggregate; s, simple crystals; −, the absence of crystals in that particular tissue. All of the species of *Dubyaea* and *Soroseris* were examined, except *D. rubra* and *S. bellidifolia*, of which little material was available, and which have close relatives among the other species. The

number of species examined in the other genera is given after the name of the genus; in every case the species were selected from subgenera and sections representing as much of the total variation within the genus as possible. When a particular type is represented by only a few species of the genus, the symbol for that type is placed in parentheses.

Dubyaea contains four histological types in respect to these characteristics. In the first, represented by *D. atropurpurea* and the Sect. AMOENAE, sclerenchyma is present, but crystals are absent from the ovary wall or nearly so. The second, represented only by *D. glaucescens*, is unique among the species investigated, since it combines the presence of sclerenchyma with that of aggregate crystals. In the third, represented by *D. hispida* and *D. oligocephala*, sclerenchyma is absent, but simple crystals occur in the ovary wall. In the fourth, the section IXERIDOPSIS, there are no sclerenchyma cells or crystals in the ovary wall.

Soroseris is more uniform. The bulk of the species conform to a type not known in *Dubyaea* in having both sclerenchyma and simple crystals. The crystals may be in the sclerenchyma cells, but are usually below or above this layer of tissue, in ordinary parenchyma cells. *S. Gillii* and *S.*

TABLE I

Distribution of sclerenchyma tissue and crystals in Dubyaea, Soroseris, and related genera.

SPECIES	SCLERENCHYMA	CRYSTALS	
		ovary wall	ovule integument
Dubyaea atropurpurea	+	−	s
D. glaucescens	+	a	s
D. hispida	−	s	s
D. oligocephala	−	s	s
D. chimiliensis	−	−	s
D. tsarongensis	−	−	s
D. amoena	+	−	s
D. gombalana	+	−	s
Soroseris umbrella	+	s	s
S. glomerata	+	s	s
S. Deasyi	+	s	s
S. rosularis	+	s	s
S. pumila	+	s	s
S. Gillii	+	s−	s
S. Hookeriana	+	−	s
Prenanthes, 13 spp.	+, (−)	s, (−)	s
Lactuca, 20 spp.	+, (−)	s, s+a a, −	s, s+a, (a)
Crepis, 30 spp.	−	a, (a+s) (s), (−)	s
Youngia, 5 spp.	−, (+)	s	s
Ixeris, 5 spp.	−	− (s)	s
Hieracium, 10 spp.	+, −	s, −	s

Hookeriana agree with *Dubyaea* Sect. AMOENAE; an interesting fact in view of the habital resemblance between these two groups of species.

Among the other genera investigated, *Prenanthes* and *Hieracium* are like *Soroseris*, *Youngia* is like *D. hispida*, and *Ixeris* is like *Dubyaea* Sect. IXERIDOPSIS. The bulk of *Crepis* species differ from any known species of *Dubyaea* or *Soroseris* in that they combine absence of sclerenchyma with aggregate crystals in the ovary wall. This is very conspicuous in *C. sibirica*, *C. kashmirica*, and other species of the subgenus Catonia which approach *Dubyaea* in habit. In all of them the aggregate crystals are particularly large and abundant, contrasting sharply with the equally conspicuous simple crystals of *D. oligocephala*. *Lactuca* is extremely variable in the distribution of both sclerenchyma and crystal types. An explanation of this variability is not yet available. Most of the Sino-Himalayan species, however, including *L. atropurpurea* and *L. Lessertiana*, the two most nearly related to *Dubyaea*, are either like *D. atropurpurea*, as is the case with these two, or are like *Soroseris* and *Prenanthes*. The available histological evidence, therefore, agrees well with that from other lines as to the relationships of the genera in question.

IX. CYTOLOGY OF THE SPECIES

Due to the difficulty of obtaining seed and of raising the plants, only a few of the species of *Dubyaea* and *Soroseris* are known cytologically. The somatic chromosome number $2n = 16$ was first reported by Babcock and Cameron (1934) for *Dubyaea hispida* (as *Crepis bhotanica*), while the root tip chromosomes of both this species and *D. oligocephala* were illustrated by Babcock, Stebbins and Jenkins (1937). In this paper the striking similarity between the chromosomes of these two species was pointed out, as well as their close resemblance to those of several species of *Prenanthes*. The hypothesis was put forward there that among primitive species of *Cichorieae* great changes in the phenotypic characteristics of the plant are accompanied by relatively slight changes in chromosome morphology and probably also chromosome structure, while in the more advanced species the reverse is often the case. This hypothesis is well borne out by the chromosomes of *Soroseris*, so far as they are known. Babcock and Cameron (1934) reported the number $2n = 16$ for a species of this genus, of which seed was received bearing the tentative identification *Crepis glomerata*. Later examination of the specimen collected with this seed (*Rock 24502*) has shown it to belong to *Soroseris Gillii* subsp. *typica*. A somatic metaphase plate of this species, from sections prepared according to the method previously described (Babcock, Stebbins, and Jenkins 1937) is illustrated in Figure 17. The only other *Soroseris* species of which it has been possible

to obtain seedlings was one sent by S. L. Ghose & Co., Darjeeling, India, under the name *Crepis glomerata*, and collected in Sikkim. Since the particular seed collection from which germination was obtained did not have a specimen accompanying it, and since the specimens accompanying other collections sent by this firm included both *S. Hookeriana* subsp. *typica* and *S. pumila*, the identity of the seedlings grown is not certain. They all died as young seedlings. Judging from the appearance of the achenes, however, they were more likely *S. pumila*. The chromosome number of this species is also $2n = 16$, and the size and morphology of the chromosomes are similar to that of *S. Gillii*, although no very satisfactory metaphase plates could be found.

Fig. 17. Somatic metaphase plate from root-tip of *Soroseris Gillii* subsp. *typica* (×2500).

As can be seen by comparing Figure 17 with the figures of *Dubyaea* previously published, the chromosomes of *Dubyaea* and *Soroseris* are very similar to each other in size and morphology as well as in number. In both genera the chromosomes have mostly median or submedian constrictions and there is little variation in size between the different members of the section. The size and morphology of the satellited chromosome pair is exactly comparable in the three species. As pointed out for *Dubyaea* (Babcock, Stebbins and Jenkins 1937) the karyotype of these species has all the characteristics of a primitive one, according to the criteria used by other workers. *Soroseris*, therefore, in spite of its specialized habit, has retained a primitive karyotype along with primitive floral characteristics, pollen grains, and ovary anatomy.

Since no further cytological information has been obtained on either *Dubyaea* or *Prenanthes*, the status of the hypothesis put forward earlier (Babcock, Stebbins, and Jenkins 1937), that the great morphological changes involved in the evolution of *Prenanthes* from *Dubyaea* have been accompanied by relatively few structural changes in the chromosomes, has not been altered. The somatic numbers of four additional Sino-Himalayan species of *Lactuca*, however, have been obtained. *L. Brunoniana* (Wall.)

Franch. (*Prenanthes Brunoniana* Wall.), *L. rapunculoides* Clarke, *L. macrantha* Clarke, and *L. Lessertiana* (DC.) Clarke all have the somatic number 2n = 16. The chromosomes resemble in size and morphology those of *L. bracteata* Hook. f. et Thoms., already illustrated (Babcock, Stebbins, and Jenkins 1937, Fig. 3e). They differ from those of *Dubyaea* and *Soroseris* in having mostly subterminal constrictions, and in the great difference in size between the members of a complement. As previously pointed out (Babcock, Stebbins, and Jenkins 1937) these are both relatively advanced characteristics, and are well correlated with the greater specialization in floral and fruit characteristics of *Lactuca*. *Dubyaea* and *Soroseris*, therefore, are cytologically nearest to *Prenanthes*. They are less similar to *Youngia* and *Lactuca*, although they have the same basic haploid number (x = 8) as most *Youngias* and many *Lactucas*. They are different from *Hieracium* in number, since this genus has the basic haploid number 9, but are rather similar to it in chromosome size and morphology. They are most different from *Crepis*, in which genus the basic haploid numbers 5 and 4 prevail, and the chromosomes have mostly subterminal constrictions (Babcock and Cameron 1934, Babcock 1936).

The stomata and pollen of all of the species of *Dubyaea* and *Soroseris* were examined since as has been noted previously (Babcock and Stebbins 1937, Sax and Sax 1937) these structures often provide evidence of polyploidy in a group, and have proved reliable in most groups of Cichorieae in which they have been tested. The only putative polyploid in *Dubyaea* is *D. glaucescens*, in which the pollen grains are nearly all 4-pored, and the average length of the guard cells is about 45μ, as compared with 28–36μ for the other species of *Dubyaea*. There are no species extant which either from the point of view of external morphology or of geographic distribution would serve as a likely diploid ancestor of *D. glaucescens*. *D. atropurpurea*, its nearest living relative, not only occupies an entirely different climatic province, separated by several intermediate phytogeographic regions from *D. glaucescens*, but in addition has larger heads, flowers and achenes, whereas the diploid ancestors of *D. glaucescens* would be expected to be smaller in these respects. The diploid ancestors of *D. glaucescens* are very likely extinct. This species may easily be the last remnant of a polyploid complex (cf. Babcock and Stebbins 1938) which was formerly more widespread and contained several species. The cytological evidence, therefore, points toward both the primitive and the relic nature of the genus *Dubyaea*.

The species and subspecies of *Soroseris* all have 3-pored pollen grains, and all compare closely in stomatal size with the known diploids, except for *S. Gillii* subsp. *hirsuta*. In this subspecies the average length of the guard cells is 42μ (specimen, *Forrest 19054*) as compared with 34μ for

subsp. *typica*. If subsp. *hirsuta* is polyploid, it is very likely of recent origin, and it has no morphological characteristics not found at least to some degree in other subspecies of *S. Gillii*.

X. PHYLOGENETIC RELATIONSHIPS OF THE GENERA

A. DUBYAEA

In regard to *Dubyaea*, the following conclusions have been reached:

1. The genus shows definite relationships to several of the larger genera of the tribe Cichorieae.
2. Its species are sharply distinct from each other morphologically.
3. They are mostly narrowly endemic to regions noted for their large number of relict endemics.
4. They are the most primitive in floral anatomy of all the Cichorieae, and among the most primitive of the Compositae in this respect.
5. Those investigated are also primitive in chromosome morphology.

These conclusions all suggest the same hypothesis: that *Dubyaea* as known at present contains the last remnants of an ancient genus which was once much larger and more widespread, and which contained the direct ancestors of some or all of the present species of *Prenanthes*, *Lactuca*, *Crepis*, *Youngia*, *Ixeris*, and *Hieracium*. Three points remain to be considered. First, what is the age of *Dubyaea;* second, what is its origin; and third, has its center of distribution always been the Sino-Himalayan region, and is this the center from which the other genera radiated?

In regard to the age of *Dubyaea*, the following suggestion can be made. *Prenanthes* is in many ways more specialized than *Dubyaea*, and appears to be a younger derivative. The minimum age for *Prenanthes* is suggested by its distribution. It has two main centers; temperate eastern Asia and temperate eastern North America. Furthermore, the most primitive species in each center, *P. acerifolia* and *P. ochroleuca* in Asia, and *P. crepidinea* in North America, are restricted in range and rare in occurrence; they have every characteristic of ancient species. *Prenanthes*, therefore, apparently belongs to that ancient temperate flora about which much has been written, and whose characteristics have been so ably summed up by Fernald (1931). Its origin can hardly be placed at later than the early part of the Tertiary period. *Dubyaea*, since it is probably older, may very well date back to the Cretaceous period.

No evidence is available on the origin of the genus. As has been said previously, it is as primitive or more primitive than any other genus of the tribe. Its origin, therefore, would have to be sought either in some other tribe of the Compositae or in another family of plants. A preliminary sur-

vey has been made of the genera of the Mutisieae, Cynareae, Senecioneae, and Vernonieae which have been suggested as related to the Cichorieae, but none has been found which, when all of its characteristics are considered, suggests the ancestry of *Dubyaea*. Equally fruitless has been an examination of various Calyceraceae, Goodeniaceae, Lobeliaceae, Companulaceae, Rubiaceae, and Caprifoliaceae. A more detailed discussion of this problem will be made in a later publication, in which the affinities of the Cichorieae as a whole will be considered, but the writer believes at present that the tribe is so old and so isolated systematically that its ancestors are extinct, and that there are no living species or groups of species which connect it with any single other modern tribe or family.

The position of the original center or centers of distribution of *Dubyaea* is suggested by the distribution of its modern relatives. None of the six larger genera mentioned above agree exactly with *Dubyaea* in their centers of distribution. *Youngia* is the closest in this respect (Babcock and Stebbins 1937), but most of its species are found in temperate regions, and it has few representatives in the subalpine region of Yunnan and the River Gorge country which is such a conspicuous center for *Dubyaea*. *Prenanthes* and *Ixeris* both have their major centers of distribution in eastern Asia, but they have few or no alpine or subalpine representatives, and their most primitive species are found farther east, in Japan and Korea. *Lactuca* has two major centers of distribution, one in the Sino-Himalayan region and one in southwestern Asia and southeastern Europe. These two centers are about equal in size, and both contain an equal number of primitive types. This suggests a polyphyletic origin for *Lactuca*, a suggestion which is supported by other evidence. *Crepis* and *Hieracium* have their major Old World centers of distribution in southwestern Asia and Europe, and are represented in the Sino-Himalayan region by only a few outlying species. The distribution of these six genera, therefore, in no way supports the hypothesis that they radiated outward from the Sino-Himalayan region.

All the evidence suggests that the present region of concentration of *Dubyaea* species never has been a real center of distribution for the genus. More likely, it has acted as a haven for the preservation of these ancient types which elsewhere have been eliminated by changes in the environment, and by competition with their more aggressive descendants. The hypothesis of Matthew (1915, p. 180) that the primitive types of a group tend to be preserved near the edges of its range, is well supported by these genera of the Cichorieae. The Sino-Himalayan region is definitely on the edge of the range of the tribe as a whole. To the south and southeast of it the country is mostly tropical or subtropical, and is occupied by only a

few scattered species of Cichorieae, while the altitudinal range of *Dubyaea* is higher than that of any other members of the tribe except for its derivative, *Soroseris*, and a few species of *Lactuca*.

Considered from this point of view, the present range of *Dubyaea* has little bearing on the place of origin of *Crepis* or of any other of the genera derived from this ancestral stock. If *Crepis* had originated in the Sino-Himalayan region, many species would have been preserved in this rich and varied flora. The actual number of *Crepis* species found is small, and they are not closely interrelated. They appear much more like migrants which from time to time have invaded the Sino-Himalayan region from elsewhere. The suggestion of Babcock (1936), that *Crepis* originated in south central Asia, is not supported by the present evidence. The suggestion of southwestern Asia, made in the same publication, is a more likely one.

In a relict genus like *Dubyaea*, the construction of anything like a phylogenetic tree is a hopeless task. As has been mentioned previously, representatives of all three sections have different primitive anatomical characteristics, and between EUDUBYAEA and IXERIDOPSIS there is nothing to choose as to primitiveness of habit and floral characteristics. EUDUBYAEA, however, has more relationships with other genera than has either IXERIDOPSIS or AMOENAE. The ancestral types of *Prenanthes*, *Lactuca*, *Crepis*, *Hieracium*, and some of *Youngia* would be associated with this first section. Species of this type, therefore, were probably widespread throughout Eurasia in early Tertiary time or earlier, and very likely had well developed distributional centers in both the western and the eastern end of the continent. IXERIDOPSIS resembles only *Ixeris* and some species of *Youngia*, so that it has probably always been confined to eastern Asia. The AMOENAE are related only to *Soroseris*, and that relationship is not very close. This anomalous section probably has always been endemic to the Sino-Himalayan region. It is perhaps the youngest of the three, and most likely dates from the uplift of the Himalaya in mid-Tertiary time. Within the sections, the interrelationships of the species are no longer clear. *D. atropurpurea*, *D. chimiliensis*, and *D. gombalana* are each the most primitive member of their section, but none is ancestral to the other species with which it is associated.

B. SOROSERIS

As has already been mentioned, *Soroseris* is most closely related to *Dubyaea*, and is most probably derived from that genus. The most obvious connection is from *Dubyaea hispida* through *Soroseris umbrella* to *S. glomerata*, *S. Deasyi*, *S. rosularis*, and *S. bellifidolia*. The assumption of this

phylogenetic line involves two difficulties. In the first place, *D. hispida* has a more reduced ovary anatomy than has any species of *Soroseris*, and in that respect may be considered more advanced. Secondly, the echinate pollen grain pattern characteristic of Sect. EUSOROSERIS, since it is found in the majority of the genera of the Compositae, is probably a more generalized and, therefore, a more primitive type than the echinolophate pattern characteristic of the Cichorieae, and found in most species of *Dubyaea* (Wodehouse 1928). The only species of *Dubyaea* which has a more primitive floral anatomy than *Soroseris*, and whose pollen grains approach those of Sect. EUSOROSERIS, is *D. atropurpurea*. This species, however, is the farthest from *Soroseris* of all in habit, size of involucres, and most other characteristics. For this reason the best hypothesis is that the ancestors of *Soroseris* were a series of species of *Dubyaea* now extinct, some of which resembled *D. hispida*, but which possessed certain primitive features now lost by their modern counterpart. *S. umbrella* was an early offshoot from the main line, which developed a habit and involucres resembling those of the Sect. EUSOROSERIS, but with much less reduction, and in addition developed the subechinolophate type of pollen grain found in the modern species of *Dubyaea*. *S. glomerata*, *S. Deasyi*, *S. rosularis*, and *S. bellidifolia* are all about equally advanced phylogenetically, and are so closely interrelated that all could have been derived from one variable species through the "fixing" of certain distinctive characteristics through geographical isolation and consequent inbreeding. *S. glomerata* is less specialized than the other three in its involucres, but more so in habit. *S. pumila* may be considered as a more specialized offshoot from the common ancestor of the four species already mentioned. The remaining two species, *S. Gillii* and *S. Hookeriana*, are doubtfully distinct from each other, and may very well be segregates from a common ancestral stock. They possess certain habital characteristics, however, not found in the *S. glomerata* group, *S. umbrella*, or even *Dubyaea hispida*. As has already been mentioned, *S. Gillii* and *S. Hookeriana* have certain features of habit and leaf shape in common with *Dubyaea tsarongensis*, *D. amoena*, and *D. gombalana*. Since these three species approach *Soroseris* in habit more nearly than do any other species of *Dubyaea*, the supposition is not unlikely that their ancestors figured also in the ancestry of *S. Gillii* and *S. Hookeriana*. On this basis, *Soroseris* must be considered as somewhat polyphyletic, in that different though related ancestral forms of *Dubyaea* figured in the origin of its species. Their relative uniformity in general habit and in the characteristics of their involucres can be explained partly through their common exposure to the rigorous selective activity of the same extreme environment, and partly through interracial and interspecific crossing during the evolution of the genus.

The "cushion" habit, consisting of greatly expanded, apparently hollow stems and closely crowded heads, is more strongly developed in *Soroseris* than in any other of the Cichorieae. This is undoubtedly due to the extreme environment to which these plants are subjected. A similar habit is found in many other Tibetan species, notably in the genus *Saussurea* of the Cynareae (Hemsley and Pearson 1902, Ward 1935). As Hemsley and Ward have pointed out, the rigors of the Tibetan climate involve not only extreme temperatures, due to the great altitude of the plateau and the surrounding mountain ranges, but in addition drouth and very high winds. Since the Tibetan plateau is the center of distribution of the genus, and its species are particularly adapted to the conditions prevailing there, the origin of *Soroseris* is most likely contemporaneous with the origin of the plateau itself. In Mesozoic and earliest Tertiary times, Tibet was under a vast inland sea (Burrard and Hayden 1934). By the end of the Eocene period the uplift of the plateau and of the Himalaya mountains to the south of it had begun, and this uplift has been more or less continuous up to the present time, at least that of the Himalaya. There must have been some time during this uplift when Tibet had a temperate climate; at this time it could have been colonized by species of *Dubyaea*. As a result of further uplift and of the rise of the Himalaya to the south, which cut off the moist ocean winds, the climate of Tibet became drier and drier. The species of *Dubyaea* were largely exterminated from that area, and only those forms which evolved into *Soroseris* could survive. This change of climate and the consequent evolution of *Soroseris* probably took place during the middle or latter part of the Tertiary period. The species of *Soroseris* then spread to dry mountain slopes on the great ranges surrounding the plateau on all sides. Their ranges were probably somewhat reduced in extent by the Pleistocene glaciation, which covered the southeastern part of the plateau, but since most of Tibet proper was too dry to be extensively glaciated (Ward 1935), *Soroseris* must have suffered less from this catastrophe than *Dubyaea*. The glaciation, however, could have been a major factor in producing the isolation necessary for the differentiation of closely related species and subspecies, such as are now characteristic of the genus, so that the present forms of *Soroseris* are probably to a large extent of Pleistocene origin.

Literature Cited

Babcock, E. B., 1936. The origin of *Crepis* and related genera, with particular reference to distribution and chromosome relationship. *Univ. Calif. Publ. Bot.* Essays in Geobot. in honor of W. A. Setchell, pp. 9–53.

———, **and D. R. Cameron,** 1934. Chromosomes and phylogeny in *Crepis* II. The relationships of one hundred eight species. *Univ. Calif. Publ. Agr. Sci.* **6**: 287–324.

————, **and G. L. Stebbins, Jr.,** 1937. The Genus *Youngia*. *Carnegie Inst. Wash. Publ.* no. 484. 106 pp.

————, **and G. L. Stebbins, Jr.,** 1938. The American Species of Crepis; their interrelationships and distribution as affected by polyploidy and apomixis. *Carnegie Inst. Wash. Publ.* no. 504. 199 pp.

————, **G. L. Stebbins, Jr., and J. A. Jenkins,** 1937. Chromosomes and phylogeny in some genera of the Crepidinae. *Cytologia, Fijii Jubl. Vol.*: 188–210.

Ballard, C. W , 1921. The Elements of Vegetable Histology. 246 pp. John Wiley & Sons, New York.

Burrard, S. G., and H. H. Hayden, 1934. A sketch of the geography and geology of the Himalaya Mountains and Tibet. 360 pp.

Diels, L., 1913. Untersuchungen zur Pflanzengeographie von West China. *Beibl. Bot. Jahrb.* **109:** 55–88.

Eames, A. J., 1931. The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. Jour. Bot. **18:** 147–188.

Fernald, M. L., 1931. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33:** 25–63.

Good, R. D'O., 1929. The taxonomy and geography of the Sino-Himalayan genus *Cremanthodium*. Benth. *Jour. Linn. Soc.* **48:** 259–316.

Hemsley, W. B., and H. H. W. Pearson, 1902. The flora of Tibet or high Asia, . . . *Jour. Linn. Soc.* **35:** 124–265.

Hooker, J. D., 1909. Sketch of the flora of British India. *Imp. Gaz. Oxford.* vol. 1: 157–212.

Hunt, K. W., 1937. A study of the style and stigma, with reference to the nature of the carpel. *Am. Jour. Bot.* **24:** 288–295.

Koch, Minna F., 1930a. Studies in the anatomy and morphology of the Composite Flower I. The corolla. *Am. Jour. Bot.* **17:** 938–952.

————, 1930b. Ibid. II. The corollas of the Heliantheae and Mutisieae. *Am. Jour. Bot.* **17:** 995–1010.

Lavialle, P., 1912. Recherches sur le développement de l'ovaire en fruit chez les Composées. *Ann. d. Sci. Nat. Bot.* 9e sér., **15:** 39–152.

Matthew, W. D., 1915. Climate and Evolution. *Ann. New York Acad. Sci.* **24:** 171–318.

Netolitzky, F., 1929. Die Kieselkörper. Die Kalksalze als Zellinhaltskörper. *Hand. der Pflanzenanat.* **3,** pt. 1a.

Stebbins, G. L., Jr., 1937a. Critical notes on *Lactuca* and related genera. *Jour. Bot.* **75:** 12–18.

————, 1937b. Critical notes on the genus *Ixeris*. *Jour. Bot.* **75:** 43–51.

————, 1937c. The scandent species of *Prenanthes* and *Lactuca* in Africa. *Bull. Jard. Bot. de L'Etat,* Brussells, **14:** 333–352.

————, 1938. A bleaching and clearing method for plant tissues. *Science* **87:** 21–22.

Ward, F. L., 1935. A sketch of the geography and botany of Tibet, being materials for a flora of that country. *Jour. Linn. Soc.* **5:** 239–265.

Wilson, E. H., 1929. China—Mother of Gardens. 408 pp. Boston, Stratford Co.

Wodehouse, R. P., 1928. The phylogenetic value of pollen grain characters. *Ann. Bot.* **42:** 891–934.

————, 1935. Pollen Grains. 574 pp. New York, McGraw-Hill Co.